THE TAPHONOMY AND PALEOECOLOGY OF THE THOMAS FARM LOCAL FAUNA (MIOCENE, HEMINGFORDIAN), GILCHRIST COUNTY, FLORIDA

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1986

ACKNOWLEDGMENTS

I would like to thank my major advisor, Dr. Ronald Wolff, for his support, guidance, and humor throughout the course of my study. I would also like to thank the other members of my committee, Drs. S. David Webb, Bruce J. MacFadden, Richard A. Kiltie, and Elizabeth S. Wing, for the many hours they spent reading this manuscript and for their many comments and suggestions.

I would also like to thank those who gave freely of their time and energy to work in the field. I am especially indebted to Richard Hulbert who spent many days collecting fossils and made countless valuable suggestions. His perseverance is greatly appreciated. Other willing and able workers included Gary Morgan, Steven Emslie, and Arthur Poyer. Russell McCarty surveyed the site and prepared many of the fossils used in this study.

Arthur Poyer helped with matrix picking and also drafted the figures in Chapter 6. I thank him for his support and friendship. I would also like to thank Dr. Douglas Jones and Roger Portell for their generosity in the loan of equipment from their laboratory. Bruce MacFadden and David Webb also made their computer facilities available to me. Gary Morgan identified many fossils for me.

Many of my fellow graduate students offered constructive advice. I thank Richard Hulbert, Mary Ellen Ahearn, Steven Emslie, David Wright, Peter Meylan and Jon Becker for their help.

Financial support received while at the University of Florida included teaching and research assistantships from the Department of Zoology, College of Liberal Arts and Sciences; curatorial and research assistantships from the Department of Vertebrate Paleontology, Florida State Museum; and research assistantships provided by my major advisor, Dr. Ronald Wolff. The Department of Zoology, College of Liberal Arts and Sciences and the Florida State Museum supplied all expendable equipment. I gratefully acknowledge these individuals, departments and institutions for their support.

I would like to extend very special thanks to a very special person, Gary Morgan, who helped with every aspect of this project and also provided much-needed moral support.

Finally, I would like to express my gratitude to my parents, Frank and Marjorie Pratt. They have always enouraged me in my pursuit of higher learning and inspired me to achieve my goals.

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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December 1986

Chairman: Ronald G. Wolff
Major Department: Zoology

The Thomas Farm locality in Gilchrist County, Florida, is a vertebrate fossil deposit of early Miocene age. Although the locality has been excavated for over 50 years, the method of formation of the deposit, the paleoecology of the fauna, and the climate and environment of north-central Florida in the early Miocene are unknown. The objective of this study was address these problems by using field excavation and taphonomic analysis to undertake a paleoecological reconstruction.

The study was divided into two major portions: field work and laboratory analysis. Excavation of the site involved recording orientation data on megafaunal elements and the collection of matrix

to screenwash for microvertebrate remains. A total of 5,000 specimens of large vertebrates was collected and identified, and over 10,000 identifiable specimens of small vertebrates were obtained from 1,400 kilograms of matrix.

Laboratory analysis included fossil identification and quantification, computerization of orientation data, and taphonomic analysis of the material. Based on the results of the taphonomic analysis, the paleoecology of the major orders of vertebrates was discussed. The environment of deposition and probable habitat and climate of the region were also determined based on taphonomic and paleoecological studies.

Results of the study indicate that the Thomas Farm vertebrate assemblage formed attritionally in a large sinkhole at least 40 meters in diameter and over 30 meters in depth. Early in its formation, the sinkhole was water-filled, and a water current moving from northeast to southwest caused alignment of long bones and transport of small elements. Water-laid deposition ceased with a major collapse of part of the limestone wall. The upper units of the site contain microvertebrate remains that accumulated in a cave. A large part of the microvertebrate fauna from these layers most likely represents a coprocoenosis.

The presence of several genera of vertebrates that today are restricted to the tropics indicate that the climate in north Florida 20 million years ago was more tropical than today. The predominance of small, brachyodont herbivores and of carnivores that are not highly cursorial suggest that the region surrounding the sink was not open grassland but was probably forested.

CHAPTER 1
INTRODUCTION

The Thomas Farm locality may certainly be counted among the best-known vertebrate fossil sites in North America. Specimens from this locality are found in several major museums, and the vertebrate fauna has been described in numerous publications (see Webb, 1981, for a complete list). The Thomas Farm is distinctive among Florida sites for a number of reasons. The vertebrate remains are incredibly numerous and consist of both large (megafaunal) and small (microfaunal) vertebrates. Localities in which all size ranges of vertebrates are found in great abundance are usually very rare. Although the site has been known for a number of years, fossiliferous sediments are still plentiful.

The history of excavation at the Thomas Farm spans over half a century. The description of the early years at the site was obtained from accounts given by T. White (1942a) and T. Barbour (1944). The Thomas Farm locality was discovered in the spring of 1931 by state geologist Clarence Simpson of the Florida Geological Survey. Mr. Simpson found scraps of fossil bone on the spoil pile from a well on the abandoned farmland of Raeford Thomas. These bones, and others found in a test pit dug to the west of the old well, were sent to Dr. George Gaylord Simpson, then at the American Museum of Natural History. Dr. Simpson identified the bones and in 1932 published a description of the site and the fossils.

No further interest was taken in the site until 1938, when Dr. Thomas Barbour of the Museum of Comparative Zoology, Harvard, made one of his regular trips to Florida. Dr. Barbour chanced to see the specimens in storage at the Florida Geological Survey and realized the great importance of the locality (Barbour, 1944). He arranged for the purchase of the 40-acre farm, and excavation began in earnest. In 1942, the fossil site and surrounding land was deeded to Dr. Archie Carr of the University of Florida Department of Zoology, who in turn donated it to the Florida State Board of Education. In the years from 1940-1958, the site was cooperatively excavated by teams from the University of Florida, the Florida Geological Survey, and the Museum of Comparative Zoology. It was during that time that the large collections were accumulated, both by Harvard and the Florida Geological Survey.

After a 5 year lapse, excavation was conducted sporadically throughout the mid 1960s into the early 1970s under the direction of Drs. Walter Auffenberg and Thomas Patton of the Florida State Museum. The 1973 season was the last time that digging was carried out over an extended period until the beginning of this study in the Fall of 1981.

Although the site has been known for 55 years, digging operations, except those of the late 1940s and early 1950s, have not been extensive. The large number of vertebrates removed during those years attests to the great richness of the site. The fossiliferous sediments are by no means depleted, and a considerable amount of digging remains to be done. The productivity of the site, coupled with the diverse fauna, and the fact that the locality is protected

by the state, make it an ideal subject for taphonomic and paleoecological analysis.

In the past, the major field efforts were geared toward the maximization of numbers of fossils removed. With the exception of the efforts of Dr. Pierce Brodkorb in 1958 and 1959, microfaunal collecting was largely ignored. The geology of the Thomas Farm locality is very complex and has never been completely understood. The mode of formation of the site and deposition of the bones has been a subject of disagreement since the locality's discovery (for a more complete discussion of this subject, see Chapter 3). The present study was designed to approach the following problems:

1. To determine, by means of systematic and controlled excavation, the geological features of the site, and the mode of deposition of the vertebrate remains.
2. To conduct a taphonomic analysis of the Thomas Farm locality--in other words, to determine which of the taphonomic factors that affect animal remains are responsible for the types of fossils deposited, their distributions, and their abundances.
3. To use information obtained from studies of the known fauna to augment the information gained in the taphonomic analysis in forming an interpretation of the paleoecology of the locality. This aspect of the study involves analysis of the vertebrate community preserved at the site, investigation of the paleohabitat in the immediate region of the locality, and assessment of the general habitat and climate of North Florida at the time of deposition of the Thomas Farm.

This study represents the culmination of five years of work, including several years of primarily field work and data accumulation, and 2 years of fossil identification, matrix sorting, and faunal analysis. It is hoped that the taphonomic and paleoecological analysis of the Thomas Farm will form a comparative basis for investigations of other early Miocene localities within the state as well as for other fossil deposits.

CHAPTER 2
MATERIALS AND METHODS

Abbreviations and Acronyms

Table 2-1 lists the abbreviations and acronyms most frequently used in this paper.

Field Excavations

Construction of the Grid

In most paleontological studies, it is advisable to construct a map of the site and establish a grid delimiting the fossiliferous sediments. These two procedures enable the paleontologist to determine the general location of a fossil or sediment within the deposit. A map published by the Florida Geological Survey in 1956 (Puri and Vernon, 1964; Puri, Yon and Oglesby, 1967) eliminated the need for construction of a new map (Figure 3-1). The elevation readings on the original map were sighted from a United States Geological Survey benchmark located on State Road 129. The map also shows several more or less permanent landmarks that were used as reference points in establishing a grid in the present excavation.

As no permanent measuring grid had ever been established at the Thomas Farm locality, it was necessary to do so before undertaking any excavation. After several prelimary visits to the site in 1981, I decided that a grid composed of 5-meter by 5-meter squares, starting from a point in the southwestern region of the site, would include the region of most fossiliferous sediments. In September of 1981, the outlay of the grid was sighted by Russell McCarty, who used a

surveyor's theodelite to determine the positions of the stakes. The stakes were placed at 5-meter intervals to the north and east, respectively, of the chosen 0 North by 0 East point. The location of this point was marked by a permanent concrete post. The major axes of the grid ran 25 meters to the north and 20 meters to the east from the datum marker.

The location of each 5-meter by 5-meter square was identified by the coordinates, in meters north and east of the ON,OE marker, of the northeast corner stake of each square (Figure 2-1a). Each of these larger squares were divided into 25 1-meter by 1-meter squares, starting from the square designated M1 located in the southeast corner. Using this system, it was possible to record the location, to the square meter, of any region of the site (Figure 2-1b).

Russell McCarty originally determined the location of the grid on the existing topographic map of the site (Puri and Vernon, 1964) by sighting from a reference point outside the site (a concrete marker placed one meter to the east of the original northern gatepost) to the ON,OE marker. At the end of the study, the ON,OE point was sighted from three other relatively permanent locations, several of which are illustrated on the topographic map. These reference points include the eastern edge of the limestone pinnacle located on the northwestern side of the drainage ditch, the westernmost edge of the enclosed south wall of the new pole barn, and a large spike driven into live oak tree in the southwestern corner of the site (Figure 2-2 and Table 2-2). A number of elevations were also shot from the ON,OE point to various regions within the excavation.

Establishing a Datum

To facilitate recording depth of sediment layers within the site, a depth datum point was established at the ON,OE marker at 50 cm above the ground surface. The sediment depth at this point was arbitrarily set at 0 cm, and all other depth measurements within the site were recorded as centimeters below this 0 depth level. Using the datum point for reference, it was possible to determine the depth for any area of the site, with the exception of the steep northern and eastern walls where no digging was planned.

At the end of the study, elevations of excavated areas were determined. The elevation of the ON,OE marker was established as 55.3 feet above sea level. At the end of the final field season, the site was cleared and a trench was dug around the edges of the grid to aid drainage, and to determine the depth and extent of remaining fossiliferous layers. Sandy matrix rich in microfauna was removed from the northern section of 10N x 10E (unit 15; see description in Chapter 3) and was taken to the grounds of the University of Florida for storage, processing and washing. Two dumptruck loads of matrix with a total estimated weight of 16 tons were removed from this upper part of the site.

Techniques in Fossil Collecting

Prior to beginning the excavation, I decided that the amount of taphonomic information obtained could be increased if the locations of fossils were mapped within the site. Accurate mapping requires that some chosen point on a bone be designated by horizontal and vertical coordinates. In many taphonomic studies, depth within the sediment is not considered, but in localities where sediments are not horizontal

or bones are collected from several different sedimentary layers, this measurement assumes great importance. It was necessary to devise a procedure by which fossils could be mapped quicky and easily. The general steps are outlined below, and will be described in greater detail in the following pages.

1. Select a bone to be mapped. This particular step is up to the judgement of the worker. Usually a fossil possessing one dimension that is noticeably longer than the others is chosen. There is a limit to the size of fossil that may be easily mapped. Some studies indicate that a length of 5 cm in one dimension is the preferred minimum size (Behrensmeyer, 1975); however, in this study, due to the abundance of small bones found at the site, I decided that the inclusion of bones down to 2 cm in length would provide additional taphonomic information.

2. Make a field identification of the bone and assign it a field number.

3. Choose a point on the bone (at one end or on some outstanding feature) from which locality measurements will be taken. These include the two horizontal measurements, recorded in some increment north and east of a reference marker, and a vertical measurement, or depth below datum. It is very important to describe the reference point carefully in the field notes, particularly the compass orientation of the bone toward the direction of the reference point.

4. With a Brunton compass, take both the bearing (the compass direction of the longest dimension of the bone) in degrees east of North, and the maximum plunge of the bone (the angle of

inclination of the longest dimension of the bone from horizontal) in degrees from horizontal, along the long axis of the fossil. It is advisable to take the bearing reading in the direction of plunge.

All workers recorded bone orientation in field notebooks. On any given day, a worker was assigned a square meter in which to excavate. This information was recorded as the meter number, from 1 to 25, within the larger 5-meter by 5-meter square. For example, square meter 5 in the southwestern edge of the 15N by 10E square was listed as 15N,10E M5. The sedimentary unit (from 1 to 17) from which fossils were taken was also recorded. When a fossil suitable for mapping (according to the requirements listed above) was uncovered, it was assigned a field number, and the reference point was chosen. Both the field number and the reference point were marked on the bone in indelible ink using a rapidograph pen. The location of the reference point was indicated by a small "x," and its description and orientation noted in the field notes. Bearing and plunge were also taken and recorded.

The location of the fossil's reference point was measured in centimeters north, and east, respectively, of the southwestern edge of the square and at some depth, in centimeters, below the 0 cm datum. Two types measuring systems were constructed during the course of this study. The first version consisted of two wooden meter sticks attached to one another at right angles (Figure 2-3a). The stick used for recording the eastern coordinate, in centimeters, was positioned along the southern edge of the square with the 0 centimeter end to the west. The ruler was leveled and anchored firmly with large nails

placed on either end and driven into the sediment. Its depth below the 0 cm datum was determined by dropping a plumb bob from a level line attached to the 0 cm datum. The length of the plumb bob and its string indicated the depth of the measuring device below the datum. The second meter stick, used to measure the northern coordinate, was equipped with a metal clip on the 0 cm end that could be snapped onto the east/west meter stick. This attachment was firm, but allowed the north/south ruler to slide along its stationary counterpart. A line level was attached to the movable stick so that it could be held horizontally when measurements were being taken.

The actual measurement was taken as follows: a plumb bob was positioned over the reference point on the fossil, and the north-south ruler was moved until it intersected the string attached to the plumb bob. The coordinates could then be read off the two meter sticks, as the number of cenitmeters, to the north and east, from the southwestern edge of the square meter. The length of the plumb bob added to the distance below the datum recorded for the stationary meter stick provided the depth reading for the bone.

This system worked well during the early phases of field work when the field crew consisted of fellow graduate student Richard Hulbert and myself. As the same square was excavated for several days at a time, the stationary ruler could be left in place indefinitely. In last year of field work (1984) Vertebrate Paleontology Collections Manager Gary Morgan, technician Art Poyer, and graduate student Steven Emslie also participated in excavation. Early in the year, members of the field crew cleared a large area for excavation. I constructed a new measuring system system that was

similar to the original in principle, but was more permanent, easier to constuct, more accurate, and covered a large area.

The major axis of the apparatus consisted of a 5-meter length of conduit pipe 1.9 cm in diameter that was treated with rust-resistant paint prior to any other modification. A 5-meter long fiberglass tape was attached to this pipe with rubber cement. At chosen north-south borders of contiguous square meters within a 5-meter by 5-meter square, short lengths of 1.9 cm diameter pipe were driven into the ground vertically. The 5-meter pipe was fitted with several PVC "T" attachments that were loose enough to slide along the length of the pipe. Snugly-fitting "T" joints were placed on the short vertical pipes as well. The longer pipe was placed into the third openings of the "T" attachments on the vertical pipes and carefully leveled with a hand level. Its distance below the 0 cm datum was measured and recorded. When this step was accomplished, the fittings on the vertical support pipes were anchored in place with hose clamps. The system at this point consisted of a ruler marking the 5-meter long east-west axis between two rows of square meters. Measuring rulers 1 meter in length were constructed using conduit pipe and 1 meter lengths of fiberglass measuring tape. A line level was attached to the top of these pipes. These shorter pieces of pipe could be fit into the "T" fittings that had been slipped onto the longer pipe prior to its attachment, and were thus able to slide the length of the 5-meter pipe at right angles to it. Using this system, it was possible to record bone measurements from 10 different square meters. Several of these measuring devices were set up in the most actively worked regions of the site. They were highly accurate and easy to assemble.

As the larger fossils were often crushed, it was frequently necessary to surround them with a plaster jacket. Orientation and positional data were recorded for all bones to be included in a particular jacket. After the jacket was removed, the depth below the datum of the sediment directly under the jacket was recorded in the field notes for the day. By taking locality measurements on the bones in the jacket, and on the jacket itself, it was possible to obtain orientation data for other bones in the jacket that had not been exposed in the field. This procedure will be further discussed shortly.

All bones encountered were collected. Bones removed without complete orientation data were placed in bags labelled with the collection date, the collector's name, the 5-meter by 5-meter square, the square meter, and the sediment level from which they were collected. Fossils smaller than 2 cm in length were obtained by collecting matrix for later screen washing. Initially an effort was made to remove some of the more consolidated sedimentary layers in blocks and prepare them in the laboratory to obtain orientation data on microvertebrate remains, but this process proved to be too time-consuming for the amount of information acquired. The majority of matrix was removed as bulk samples.

During the first field season, a random numbers table was used to select 25 random square meters for sediment collection. I rapidly realized that the amount of matrix involved was more than could be collected and processed by the number of workers available. The alternate approach taken was to collect large quantities of each of the major sediment layers encountered. The total amount of sediment

collected, washed, and picked for use in this study was approximately 1400 kg dry weight. The amount of sediment washed and picked from each sediment layer is shown in Table 2-3. In general, the thicker the layer, the larger the representative sample. Large amounts of sediment from unit 15 were washed because this massive layer was extremely rich in microfauna.

Field Sedimentology

As few previous descriptions of the Thomas Farm locality have included information concerning site stratigraphy, an effort was made to document each sediment layer encountered and its characteristics. The major beds are composed of sand and clay layers, and the bones are definitely concentrated in layers. The layers were named with reference to the major bone-bearing sediments. The lowest level encountered was designated as unit 1, the highest, unit 17. The total thickness of exposed sediment is about 3.5 meters.

With the exception of material collected from spoil, the sediment level from which a fossil was recovered was recorded in all cases. Sediment samples for screenwashing, sediment analysis, or pollen analysis were collected from specific depths within given square meters. All data and observations were recorded. Strikes and dips of beds were taken frequently throughout the course of the study, as were determinations of depths below the datum and thicknesses of particular sedimentary units. Strike is defined as the bearing, in degrees east of North, of a horizontal line on an inclined plane (in this case the sedimentary layer). Dip is the inclination of the line, in degrees from horizontal, of the greatest slope of an inclined plane. It is measured perpendicular to the direction of strike. This information

was used to construct the stratigraphic section shown in Chapter 3 (Figure 3-1).

Laboratory Procedures

Megafauna, Geology, and Taphonomy (Chapters 3, 4, and 5)

Fossil preparation. All bones collected in the field were returned to the laboratory for cleaning, repair, identification, and cataloging. Fossils were washed, air-dried, and identified as completely as possible using Florida State Museum specimens for reference. Care was taken to keep all relevant field data associated with the elements. Jackets were prepared in the fossil preparation lab by technicians and by myself. It was possible to obtain locality data on bones that were included in jackets but had not been exposed in the field by tracing the outline of each bone on clear plastic as it was uncovered in the laboratory. Bones with orientation data were labelled as such on the tracing. By noting the relative depth of a bone within the jacket, it was possible to estimate its actual depth below the 0 cm datum by referring to the depth measurement taken in the field at the bottom of the jacket. When a jacket was completed, the positions and orientations of the bones without field numbers could be calculated by determining their orientations relative to those bones in the jacket for which data had been recorded. The only measurement that could not be obtained was plunge of the bone.

Computerization. All information recorded for fossils greater than 2 cm in length was translated into numerical codes for computerization. The fossils were sorted into three major groups: those with field numbers and complete locality and positional data, those collected in the field with square meter and level data only,

and those collected from the matrix, but belonging to animals whose remains for the most part are large enough to be identified in the field (small carnivores and artiodactyls). The first group was designated and identified using field numbers assigned at the time of collection, the second group was assigned identification numbers beginning with the letter "Z", and the third group was designated by numbers prefaced by the letter "M". This approach was taken as an alternative to cataloguing the fossils because the letter prefix facilitated recognition of the group to which the fossil belonged, and because a number of the fossils identified for use in the study are fragmentary and will not be catalogued. The coded data were entered and stored using the Northeast Regional Data Facility (NERDC). Data categories were as follows:

1. Identification data: bone identification number, family, genus, species, type of element, side (right or left), portion of element (complete, proximal, distal, and so on), greatest length of element.
2. Provenience data: sedimentary unit, 5-meter by 5-meter square, square meter, location within meter (in cm), depth below datum.
3. Orientation data: side of element facing up in field (medial, lateral and so on), uncorrected bearing, uncorrected plunge, corrected bearing, corrected plunge, compass orientation of reference point.

A total of 5,000 megafaunal entries was made. Data were analyzed and manipulated using Statistical Analysis System programs (SAS User's Guide, 1982). Sorting procedures were used to sort elements by data categories such as taxon, element type, or sedimentary unit. Graphic

programs were used to construct histograms of preferred orientations, to plot bone locations within square meters or larger areas, and to calculated minimum numbers of individuals and numbers of specimens per taxon, densities, and relative representations of bones.

Mapping. Bones with field numbers and specific locality measurements were mapped by hand on two-dimensional maps of the square meter and sediment level from which they were removed. Upon completion of a square meter map (all bones and sediment of a given layer removed from that square), the map was photocopied on a clear acetate sheet. The see-through map could be placed as an overlay on maps of lower sediment levels from the same square meter to show overall bone concentrations and orientations for a given excavated region. The reference points of bones were also plotted on north/south stratigraphic sections of the site to show relative bone concentrations within different sedimentary levels. This procedure proved to be of use in providing a check on the field identification of the sedimentary unit.

Modern taphonomic studies. Although some experimental studies dealing the effects of running water on bone orientation and dispersal have been undertaken by previous workers (Voorhies, 1969; Behrensmeyer, 1975; Korth, 1979; Pratt, 1979; Hanson, 1980), it was necessary to conduct additional studies on skeletal element behavior in standing and moving water. I observed bone hydraulic behavior in a series of experiments using modern skeletal elements. Deer and horse bones that retained grease, as well as elements that had been naturally weathered, were placed in water, and water uptake rates were monitored by recording weight gains to bones after varying periods of

immersion. The inital tendency for an entire bone or one end of a bone to float was also noted, as was the bone's settling orientation through standing water.

I also analyzed hydraulic behavior of bones in moving water using two different experimental procedures. In one, conditions similar to those that occur in periodic filling and draining of a pond or sinkhole were simulated using a large (67 cm by 3 meter long by maximum 0.5 meter deep) wooden sink. The sink had a sloping bottom (degree of slope 10 degrees), and a drain 15 cm in diameter at the lower end. The bottom of the sink was covered with a 5 cm thick layer of fine sand. After the sink was slowly filled with water I dropped selected skeletal elements into it. The original positions of the bones at rest were noted. Release of the plug created a strong current. Movements of the bones, if any, were measured, and changes in their positions were noted. Each experiment was repeated three times.

I observed fluvial effects on bone orientation and dispersal by dropping elements into a small creek on the University of Florida campus. Flow velocity averaged 35 cm/second along the length of the stream used in these experiments. Skeletal elements of Recent deer and horses were placed in the stream in selected groups corresponding to their Voorhies dispersal groups (Voorhies, 1969), and their transport was observed. The length of time required to move one element relative to the length of time before other elements were moved by the current was noted, as well as the element's position during transport, and its final resting orientation. Each set of bones was observed in three trials. Results of these studies were

consulted in the comparison of fossil bone orientations with those expected under moving water conditions.

Bone orientation. Orientation patterns of fossil skeletal elements were determined using a number of techniques first used by geologists but now employed in taphonomic studies (Voorhies, 1969; Hill and Walker, 1972; Saunders, 1977; Shipman, 1981). The presence of preferred bone orientation can be determined by construction of a mirror-image rose diagram. The bearing records a bone's compass orientation from 0 to 360 degrees east of North. If bearing only is considered, each bone has two possible compass orientations 180 degrees apart. For example, it is assumed that a bone bearing 10 degrees east of North is oriented in the same direction as one bearing 190 degrees east of North. The rose diagram is constructed by dividing 180 degrees (half a circle) into 18 10-degree wedges. The length of a wedge reflects the percentage of bones oriented within that 10-degree increment. Each wedge is duplicated on the other side of the 180 degree axis, forming the mirror-image rose diagram (Shipman, 1981). Rose diagrams were constructed for all bones from the locality with appropriate data, for long bones only, for bones from specific sedimentary layers, and for various types of elements. Orientation patterns of bones were compared to the pattern of bones in a uniform, or non-preferred orientation pattern (random orientation pattern of Shipman, 1981) using the Chi-square goodness of fit test (Sokal and Rohlf, 1981:710). Orientation patterns were considered significantly different from uniform at the $P = .01$ level. Orientation to a preferred end was also assessed by determining percentages of orientations of ends of bones to each of the four compass points.

Bone bearings and plunges were plotted on stereonets using the technique for plotting bearings and plunges of lines (Ragan, 1973:95; Voorhies, 1969). Stereographic plots were made of all elements with orientation data, and of long bones only.

Faunal composition. Using a computer-generated list as a reference, I determined the numbers of specimens per species of megafaunal taxa both within each major sedimentary unit and for the recently excavated portion of the site as a whole. Broken fossils were examined to see if contacts with other broken elements of the same type could be made. Minimum numbers of individuals (MNI) per species were calculated, based on the most numerous identifiable element of a species (Shotwell, 1955). The similarities in faunal composition and relative abundances of megafaunal taxa between layers were assessed by the R x C test of independence (Sokal and Rohlf, 1981:745). Faunal samples were considered significantly different from one another at the P = 0.01 level.

Relative representations of skeletal elements. The abundances of various types of elements found in an assemblage are of use in determining the agents involved in forming a particular assemblage (Voorhies, 1969; Wolff, 1973; Korth, 1979; Maas, 1985). The relative representation of an element is calculated by determining the number of that type of element present relative to the number expected to be found based on the minimum number of individuals present. The formula is

$$\frac{\text{number of elements observed}}{\text{number of elements expected based on MNI}} \times 100$$

(Voorhies, 1969; Wolff, 1973; Korth, 1979). Relative representations of skeletal elements of the equid Parahippus leonensis were

calculated. Relative representations of elements (also known as percentage preservations) were determined for each major bone-bearing layer, and sometimes several similar layers were grouped to obtain larger sample sizes. Percentage preservations of fossil elements were compared to relative representations of modern skeletal elements accumulated by carnivores. The values were compared statistically using the R x C test of independence (Sokal and Rohlf, 1981:745). Relative representation patterns of fossil and recent assemblages were considered significantly different from one another at the P = 0.01 level. Abundances of element types were also compared with those seen in fluvial deposits (Voorhies, 1969; Behrensmeyer, 1975; Korth, 1979; Hanson, 1980).

Hydraulic equivalents. The comparison of a bone to a sedimentary particle such as a quartz grain for which fluvial behavior has been determined empirically (Allen, 1965), allows one to predict current velocities necessary to cause transport of that bone (Behrensmeyer, 1975; Korth, 1979; Pratt, 1979). The diameter of a grain (or sphere) of quartz that ideally should be transported by a current sufficient to cause transport of the bone is determined using the following formula:

$$dq_n = (P_b - 1)(\ 1.91\ V_b / \ 1.65)$$

where dq_n is the diameter, in centimeters, of the equivalent quartz grain, P_b is the bone density, and V_b is the bone volume. I determined the volume of Parahippus leonensis elements using water displacement. The density of a fossil bone is seldom the same as its density prior to fossilization, so the density values used in the calculation are determined for bones of modern mammals. I calculated

densities of modern Equus elements by weighing both dry bones and bones that had been allowed to soak in water for a day. The "wet" or "dry" weight of the element divided by its volume (determined by water displacement of waterlogged elements) provided both "dry" and "wet" density values. If I was not able to determine density of a particular element, I used the density calculations given by Behrensmeyer (1975:570) for zebra elements.

Geology experiments. In an effort to observe and document the sequence of events that occur in the deposition of a debris cone, I constructed a small-scale sinkhole replica in the laboratory using a 10-gallon aquarium tank filled with water. The top of the tank was covered, except for an opening 5 cm in diameter through which sediment was introduced. The opening was located near one side of the tank so that a complete cone did not form, and formation of the layers could be viewed through the glass. The initial shape of the cone was determined by introduction of a limestone "rubble layer". I subsequently dropped sand, clay, or pebble sediments through the opening periodically. Photographs of the debris cone may be seen in Chapter 3.

Microfaunal Taphonomy (Chapter 5)

Sediment processing. Matrix to be screenwashed was collected in plastic 50-pound feed sacks and returned to the Florida State Museum. Damp matrix was stored in large flat trays, where it was air-dried for a period of at least two weeks. I weighed each sample to the nearest gram on a 25 kg beam balance and washed the sediment through a set of three nested screens. The top screen was constructed of 4-mesh hardware cloth (16 openings to the square inch). The second screen

was composed of standard 16-mesh window screen (256 openings to the square inch), and the bottom screen was constructed of 24-mesh brass screen (576 openings to the square inch). During the first week of screenwashing operations, residue of a 25 kg sample of sediment that had passed through the finest screen was collected and examined for identifiable vertebrate remains. No identifiable bone was found; so it was assumed that the brass screen was sufficiently fine to catch the majority of identifiable vertebrate remains.

After washing, the matrix residue was air-dried in a drying cabinet for 1 to 2 days or until it was dry to the touch. Occasionally, the matrix would contain clay particles after one washing, and a second washing was required. The second treatment was almost always sufficient to break down any remaining clay particles. Each of the 3 fractions of a matrix sample was weighed. I recorded all data, including sediment weight prior to and following washing, the date collected, the type of sediment, and its location within the site. All matrix fractions were picked for identifiable bone. Arthur Poyer picked large quantities of window-screen matrix from unit 15, and I picked all of the coarse and fine matrix from all units, as well as window-screen residue. A binocular dissecting scope was always used in the examination of the finest matrix, and bones were picked from the window matrix with the aid of a magnifier or a dissecting scope. Bones recovered from window and brass screen were lumped when the sample was analyzed. In a few samples, the bones collected from different size sediment fractions were kept separate as a means of determining the number of additional identifiable specimens obtained by use the fine brass screen.

Abundances. After removing all potentially identifiable fossils from the matrix, I sorted the bones according to taxon and identified them as completely as possible. Numbers of specimens of each taxon were counted, and MNI were calculated. These calculations (when possible) were determined for each sediment layer from which at least 50 kg of matrix had been collected. Faunal composition of the various layers was compared statistically using the R x C test of independence (Sokal and Rohlf, 1981).

Relative representations. I counted elements of the rodent Proheteromys floridanus and anuran elements from each sediment layer to determine relative representations of skeletal elements for these groups. The relative representation values of rodent elements in unit 15 were compared with those of elements in modern scatalogical accumulations using the R x C test of independence (Sokal and Rohlf, 1981).

Comparative studies. Fossil microfaunal elements were examined under high magnification of a binocular dissecting scope. Breakage of bones was assessed as resulting from either pre-fossilization or post-fossilization factors, based on descriptions in Behrensmeyer (1975), Korth (1979), Shipman (1981), and Binford (1981). Fossil bones that showed pre-fossilization breakage and evidence of acid destruction were compared with recent bones from scats of coyote, bobcat, and weasel, as well as from pellets of sharp-shinned hawk, red-tailed hawk, screech owl, barn owl, and great horned owl.

Hydraulic equivalents. I determined quartz grain equivalents of major elements of modern Peromyscus and Rana. Due to the difficulty encountered in determining volumes of small elements, the equivalent

quartz diameter (dq_e) rather than the nominal quartz diameter (dq_n) was calculated. The equivalent diameter indicates the size of the quartz grain that achieves the same terminal settling velocity as the bone in question and therefore hypothetically would be transported at a current velocity similar to that required to move the element (Behrensmeyer, 1975; Korth, 1979). Bones were immersed in water until waterlogged (1-3 days), then dropped one by one into a 50 cm tall graduated cylinder filled with room-temperature water. Each bone's rate of descent through standing water was timed with a stop-watch accurate to 0.01 second. The bones were allowed to fall for 15 cm before timing began. The mean fall velocity, in cm/second, was determined from 10 trials with each bone. The equation for calculating the equivalent diameter is

$$dq_e = .000928\ vs^2$$

where dq_e is the diameter of the equivalent quartz grain, in centimeters and vs is the settling velocity of the skeletal element.

Paleoecological Studies (Chapters 6 through 10)

Herpetofauna (Chapter 6). Numbers of specimens per taxon and MNI per taxon of amphibians and reptiles were determined as described previously. MNI of anurans were based on ilia. MNI of Notopthalamus were based on on the number of pre-caudal vertebrae. Pre-caudal vertebrae can be distinguished from caudal vertebrae, and the number of precaudal vertebrae is less variable than caudal vertebrae. I examined 5 modern Notopthalamus skeletons in the UF Herpetology collection to determine that the standard number of pre-caudal vertebrae is 14. Therefore an MNI of 1 Notopthalamus based on vertebrae requires the presence of at least 14 pre-caudal vertebrae.

MNI of lizards were based on dentaries. Identification was to the family level only, so it is likely that the actual numbers of individuals is higher than indicated in this study. When possible, MNI of snakes were based on cranial material also, but most individuals were counted on the basis of vertebrae. Snakes were also identified to family only, and estimates of their abundances are almost certainly low.

Anuran population structure and length of larval stage are just two features of frog ecology that are related to body size. Dr. P. Meylan (pers. comm.) has shown that the height of the acetabulum of the ilium is correlated with snout-vent length. I measured ilia of recent anurans in the UF Herpetology collection. The acetabular height measurement is shown in Figure 2-4. Specimens were measured to the nearest 0.01 mm using a Gaertner measuring microscope. A total of 72 specimens representing 4 families and 24 species were measured. Acetabular height was plotted against snout-vent length for each frog measured and regression lines were calculated using least-squares linear regression. A regression was calculated for each of three families measured: Bufonidae, Hylidae, and Ranidae.

Acetabular height was also determined for fossil anuran ilia from each of the major sediment layers. A total of 382 specimens were measured; 172 Bufo praevius, 30 Acris barbouri, 95 Hyla goini, 2 H. miofloridana, 2 H. sp., 72 Rana abava, 8 Rana bucella, and 1 Scaphiopus cf. holbrooki. Acetabular heights were converted to snout-vent lengths using the appropriate regression equation.

Rodentia (Chapter 8). MNI of the most common rodent Proheteromys floridanus were based on upper incisors. MNI of other rodents were

based on cheekteeth. The data used in the calculation of the head and body length to body mass least-squares regression were obtained from specimen tags on FSM Mammalogy collection specimens and a printout of the USNM Mammalogy collection of heteromyid holdings. Measurements of modern and fossil specimens were taken using a Gaertner measuring microscope (measurement to 0.01 mm) and steel metric dial calipers (measurement to 0.1 mm). Measurements taken in this study are as follows (Figure 2-6):

1. Tranverse width of M_1 taken along the greatest transverse width of the tooth.

1a. Anterior-posterior length of M_1 taken along the greatest anterior-posterior length of the tooth.

2. Labial crown height of M_1 taken from the central valley to the base of the crown.

3. Tranverse width of the incisor taken across the anterior enamel-covered section parallel to the alveolus.

4. Incisor thickness taken across anterior-posterior dimension of incisor perpendicular to measurement #3.

5. Proximal breadth of humerus taken across the greatest transverse dimension of the head.

6. Distal breadth of humerus taken across the greatest transverse distal dimension.

7. Greatest length of humerus.

8. Greatest length of radius.

9. Ulna olecranon length taken across the anterior edge of the olecranon.

10. Length of ulna distal to semi-lunar notch.

11. Breadth of head of femur.

12. Greatest length of femur.

13. Proximal breadth of tibia taken across greatest transverse proximal dimension.

14. Greatest length of tibia.

15. Distal breadth of tibia taken across greatest transverse distal dimension.

Recent specimens were obtained from the FSM Mammalogy collection and are listed in Chapter 8. Regressions of cranial and postcranial measurements of modern rodents against head and body length or body mass were determined using least-squares linear regression analysis. These equations are used in the estimation of body size of fossil rodents. Fossil specimens were obtained from the randomly collected matrix samples. Additional specimens were added from previously collected material.

Carnivora (Chapter 9). Measurements were taken on Recent and fossil carnivore elements as a basis for morphometric analysis. Measurements were taken with metric dial calipers (measurements to 0.1 mm) and are as follows (Figures 2-6 through 2-8):

1. P^1-P^3 length.

2. P^4-M^2 length.

3. Anterior-posterior length of M^1.

4. Tranverse width of M^1.

5. P_1-P_4 length.

6. M_1-M_3 length.

7. Depth of mandible below M_2.

8. Greatest length of M_1.

9. Proximal breadth of humerus.
10. Greatest length of humerus.
11. Minimum breadth of humerus.
12. Distal breadth of humerus.
13. Transverse breadth of trochlea.
14. Greatest length of radius.
15. Distal breadth of radius.
16. Minimum breadth of radius.
17. Proximal breadth of radius.
18. Greatest length of olecranon.
19. Thickness of ulna distal to semi-lunar notch.
20. Greatest length of ulna.
21. Proximal breadth of head of femur.
22. Greatest length of femur.
23. Distal breadth of femur.
24. Minimum breadth of femur.
25. Greatest length of tibia.
26. Distal breadth of tibia.
27. Proximal breadth of tibia.
28. Greatest length of calcaneum.

Recent comparative specimens were obtained from the FSM Mammalogy collection. Fossil specimens include both recently and previously collected material. Body size estimates were determined using ZAP software, a program designed for zooarchaeologists by I. Quitmeyer and S. Haile, Florida State Museum Zooarchaeology Department.

Ungulates (Chapter 10). Measurements were taken on fossil perissodactyls and artiodactyls using steel metric dial calipers

(measurements to 0.1 mm). Measurements are as follows (Figure 2-9):

1. Anterior-posterior length of M^2.
2. Transverse width of M^2.
3. Anterior-posterior length of M_2.
4. Transverse width of M_2.
5. Unworn crown height of M_3.
6. Length of lower molars measured at junction of cement and crown.

Fossil ungulates measured in this study are from the FSM Vertebrate Paleontology collection. The hypsodonty index was calculated as the ratio of measurement #5 to measurement #3 (Janis, 1984). M^2 area was determined by multiplying anterior-posterior length by tranverse width.

Community Analysis (Chapter 11)

As a means of estimating population densities of Thomas Farm mammals, the raw abundance (MNI per species) of each species was plotted against its estimated body mass. Raw abundances were also corrected for loss incurred by pre-burial surface destruction as discussed by Damuth (1982). The corrected abundance is determined by the following formula:

$$\log d_i = .68(\log W_x - \log W_1)$$

where W_x is the body mass, in grams, of the largest species in the community, and W_1 is the body mass of the species in question. The product of d_i and the raw abundance provides the corrected abundance. Corrected values were also plotted against body mass estimates.

Ecological diversity of the mammals from the Thomas Farm locality was compared with mammalian diversity in selected recent habitats

(Fleming, 1973; Andrews, Lord, and Nesbit Evans, 1979; Vrba, 1980). Ecological diversity was calculated by:

$$H' = p_i \log_e p_i$$

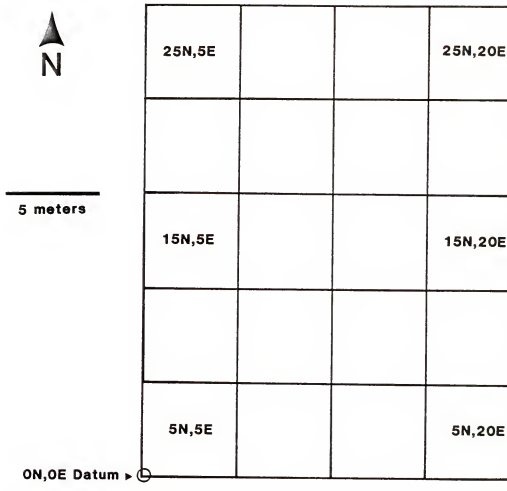
where p_i is the proportion of individuals (or in this case, species), within each class of the category (Pianka, 1966; Fleming, 1973; Whitaker, 1975; Andrews et al. 1979). Equitability (E) of the distribution of the classes within the category is defined as:

$$E = H' / H'_{max}$$

where H'_{max} is the natural log of the number of classes within the given category.

Figure 2-1. The Thomas Farm grid system. a) Arrangement and identification of 5-meter by 5-meter squares; b) Numbering of 1-meter by 1-meter squares.

A


N
25N,5E
25N,20E
5 meters
15N,5E
15N,20E
5N,5E
5N,20E
0N,0E Datum

B

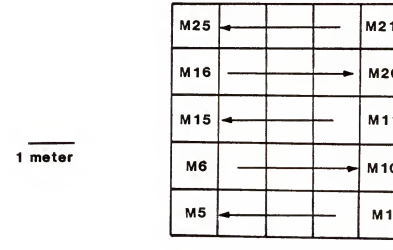

M25
M21
M16
M20
M15
M11
M6
M10
M5
M1
1 meter

Figure 2-2. Map of Thomas Farm showing outline of excavation and grid, and landmarks used for establishing location of ON,OE datum; 1, east edge of limestone pinnacle in northern drainage trench; 2, cement marker by northern gatepost; 3, live-oak tree at southwestern corner of grid; 4, western edge of siding on southern face of pole barn.

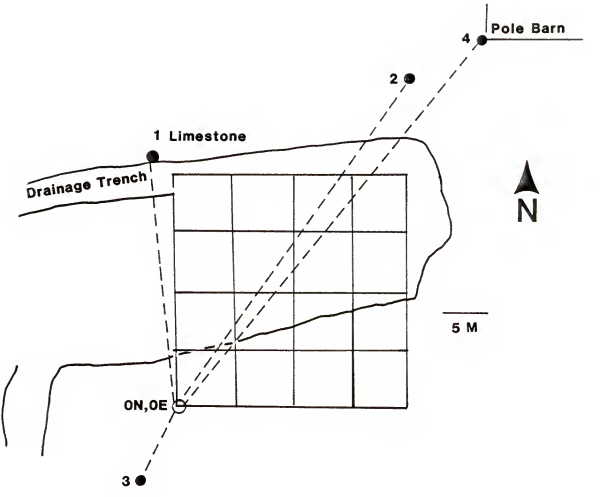
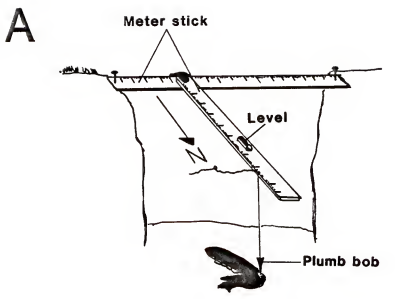

Pole Barn
4
2
1 Limestone
Drainage Trench
N
5 M
0N,0E
3

Figure 2-3. Measuring devices used to obtain bone mapping data. a) Measuring device used in 1-meter by 1-meter square; b) System used to measure bones within 5-meter by 2-meter area. See text for a complete description.


A
Meter stick
Level
N
Plumb bob

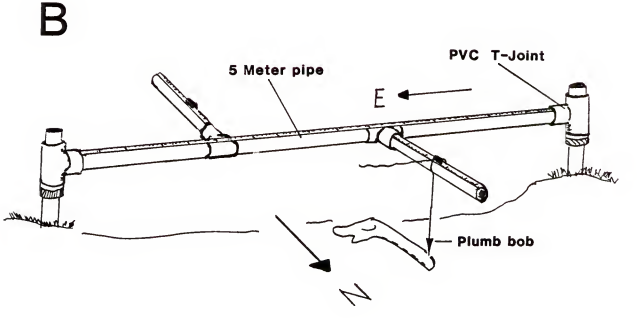

B
PVC T-Joint
5 Meter pipe
E
Plumb bob
N

Figure 2-4. Schematic diagram (not to scale) illustrating acetabular height measurement (HA) of an anuran ilium. Anterior to left.

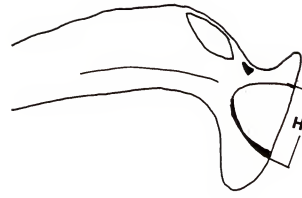

HA

Figure 2-5. Schematic diagram (not to scale) illustrating measurements taken on rodent skeletal elements. a) Left lower molar; b) Left incisor, lateral view; c) Left humerus; d) Left radius, anterior view; e) Left ulna, lateral view; f) Left femur, posterior view; g) Left tibia. See text for description of measurements.

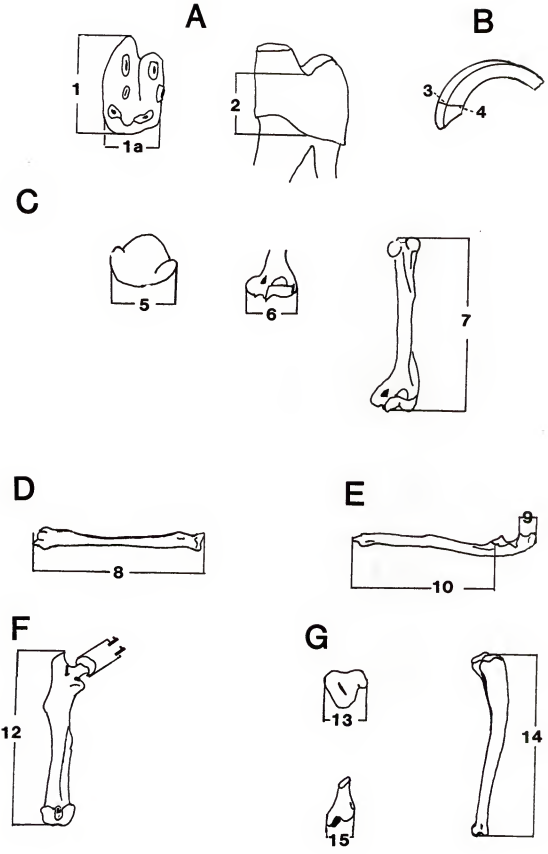

A
B
C
D
E
F
G
1
1a
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Figure 2-6. Schematic diagrams (not to scale) illustrating measurements taken on carnivore crania. a) Maxilla, occlusal view; b) Left M^1, occlusal view; c) Left mandible, lateral view; d) Left M_1, occlusal view. See text for description of measurements.

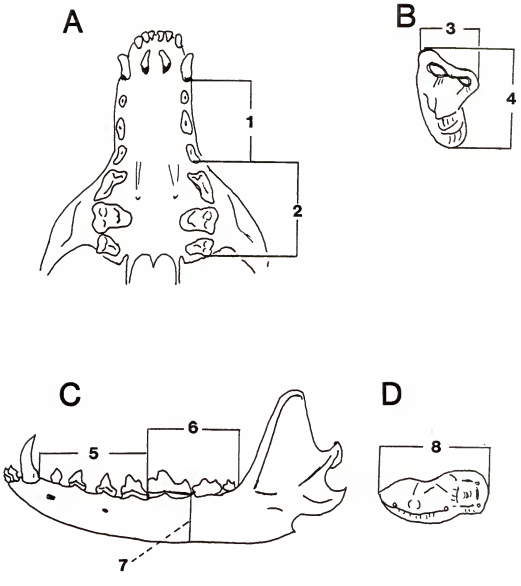

A
1
2
B
3
4
C
5
6
7
D
8

Figure 2-7. Schematic diagrams (not to scale) illustrating measurements taken on carnivore forelimb elements. a) Left humerus, proximal view; b) Left humerus, anterior view; c) Left distal humerus, anterior view; d) Left radius, anterior view; e) Left radius, cranial view; f) Left ulna, lateral view. See text for descriptions of measurements.

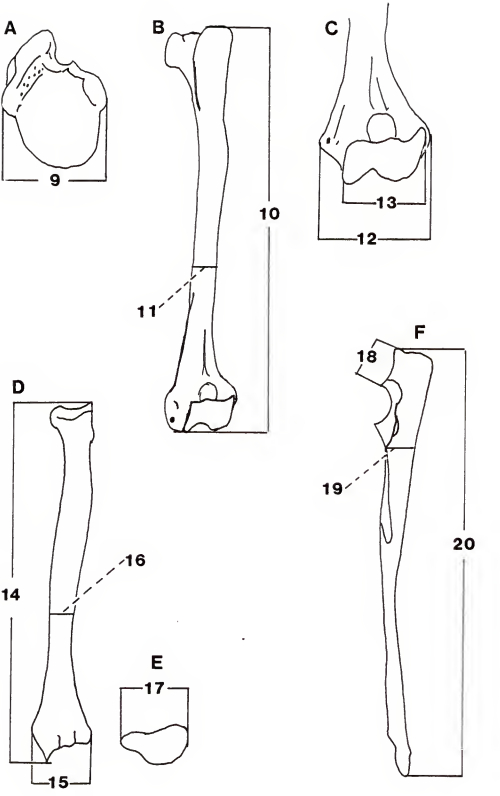

A
9
B
10
11
C
13
12
D
14
16
15
E
17
F
18
19
20

Figure 2-8. Schematic diagrams (not to scale) illustrating measurements taken on carnivore hindlimb elements. a) Left femur, posterior view; b) Left tibia, anterior view; d) Left tibia, proximal view; d) Left calcaneum, anterior view. See text for descriptions of measurements.

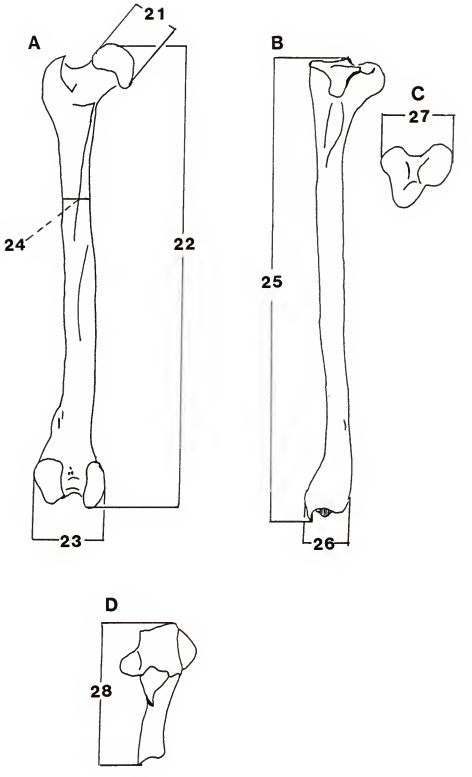
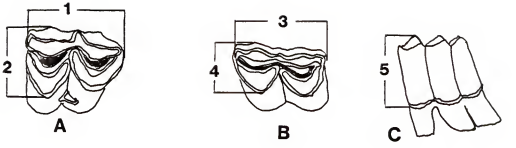

A
21
24
22
23
B
25
26
C
27
D
28

Figure 2-9. Schematic diagrams (not to scale) illustrating measurements taken on fossil ungulates. a) Left M^2, occlusal view; b) Left M_2 occlusal view; c) Left M_3, labial view; d) Left mandible, lateral view. See text for description of measurements.


1
2
A
3
4
B
5
C

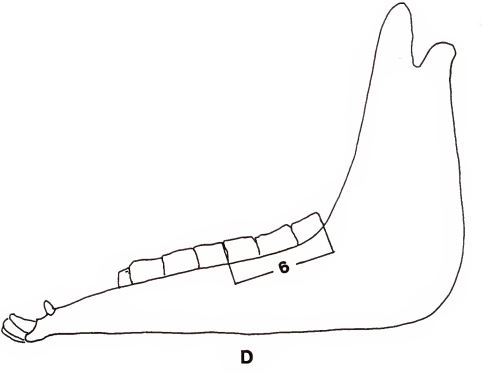

6
D

Table 2-1. Abbreviations and acronyms used in this study.

Acronym	Institution/Collections
AMNH	American Museum of Natural History
FGS	Florida Geological Survey
FSM	Florida State Museum
MCZ	Museum of Comparative Zoology, Harvard
UF	University of Florida collections
USGS	United States Geological Survey
USNM	United States National Museum

Abbreviation	Term
cm	centimeter
dq_e	equivalent quartz grain diameter
dq_n	nominal quartz grain diameter
g	gram
kg	kilogram
m	meter
M	designation for square meter of grid
$M^1(2,3)$	upper molars
$M_1(2,3)$	lower molars
M.	Musculus
MNI	Minimum Number of Individuals
N	Number (of individuals)
NERDC	Northeast Regional Data Center
SAS	Statistical Analysis System

Table 2-2. Locations of references points used to mark ON,OE datum point.

Reference Point and Description	Angle (east of N) from ON,OE	Distance (m) from ON,OE
1. Limestone pinnacle, N. trench	353	21.95 (72 ft.)
2. Cement marker by N. gatepost	37	38.71 (127 ft.)
3. Live-oak, SW edge of site	206	7.15 (23.5 ft.)
4. Siding, southwest edge of pole barn	39	43.83 (144 ft.)

Table 2-3. Dry weights, in kilograms, of matrix washed in the course of this study.

Unit	Sediment Type	Total Dry Weight (kg)
5	sandy clay	214
6	gray clay with limestone cobbles	121
7	clay and sandy clay	68
8	boulders, white sand, clay and sandy clay	104
9-10	white sand	30
11	limestone boulders and sand	227
12	fine gray sand	33
15	limestone sand	646
	TOTAL	1443

CHAPTER 3
ENVIRONMENT OF DEPOSITION

Previous Excavations and Interpretations

Although the Thomas Farm locality was discovered over fifty years ago, and has been worked periodically since that time, information concerning the actual excavation is limited. Much of this historical account of the site has been gleaned from various publications, notes, photographs, and anecdotal references.

Field work at the site was initiated in 1931 by FGS geologists Clarence Simpson and G. M. Ponton. An account of the results of their work, later incorporated into Dr. George Gaylord Simpson's study of the Thomas Farm mammalian fauna (1932), included a description of a 6-foot stratigraphic section consisting of 9 sedimentary layers. The section was obtained from a trench that was evidently dug on the western edge of the site, as a major feature of the eastern portion of the site, the boulder bar, is not mentioned in the description.

Dr. G. Simpson offered two alternative hypotheses concerning the mode of deposition of the locality. In the first, he suggested that the fossils had accumulated as a result of the breakdown of the marine Hawthorn Formation and subsequent reconcentration of the bony elements in the underlying Ocala Limestone. This idea was immediately discarded, as no Miocene marine fossils are known from the locality. The second interpretation was one that would be repeated and elaborated upon in subsequent years, "the sinkhole hypothesis." Its basis was simply that prior to any excavation, the fossiliferous

sediments were found in a large circular depression about 250 feet in diameter and roughly 15 feet lower in elevation than the surrounding ground surface (Simpson, 1932). It was suggested that the depression marked the site of an ancient sinkhole. According to Simpson's paper, this interpretation was supported by the fact that the bones were concentrated in specific layers and there was no obvious evidence of fluvial transport of the fossils.

After a 6 year hiatus, excavation at the site was renewed in the late 1930s by field parties from the Museum of Comparative Zoology at Harvard University. In 1942, Theodore White published a map and a stratigraphic section of the site (White, 1942a:Plate 14) based on analysis of auger samples taken by Clarence Simpson. The exact placement of the "dig" cannot be identified with certainty, as White's map contains no recognizable landmarks. The original map from which the published version was constructed is also lacking any points of reference by which the position of the dig may be determined. Based on the stratigraphic section and photographs of the locality taken in the 1940's (Barbour, 1944), it seems likely that much of the excavated region was in the vicinity of the boulder layer.

The stratigraphic section published by White (1942a) does not contain fine-scale sedimentological details compared with what is known about the sedimentary layers at present, but it does provide important documentation of the early excavations undertaken by MCZ workers. Several of the sedimentary layers pictured in White's section have not been encountered in the present excavation. The clayball layer located on the easterly surface of the boulder bar was probably removed in earlier excavations, and the bedrock limestone

reportedly found about 7 feet below the surface in the western portion of the site has not been relocated. As the presence of the limestone was based on one auger sample, and no information was given as to the type of limestone found, it is possible that it represents a limestone boulder rather than a solid wall of limestone. White also discussed the presence of lens of phosphatic sandstone in the southeastern edge of the site. He identified this layer as the marine Hawthorn Formation. If this unit is in place today, it is in a region of the site now completely covered by large shrubs and trees.

White did not favor Ponton's and C. Simpson's earlier view (G. Simpson, 1932) that the site was formed as a result of sediment deposition in a sinkhole, suggesting instead that the sediments represented a sequence of several cycles of cutting and filling by a fluvial system. He cited the presence of lenticular clays, the lack of sorting of the sediments, and the presence of the boulder bar as support for this interpretation. White proposed that a stream initially carved a channel in the Ocala limestone, and eventually silted up, depositing sands and bones as the current slowed. The stream was later rejuvenated, and current velocities increased sufficiently to cause transport and eventual deposition of the boulder bar. Following this major depositional event, the current again slowed and clayballs and sand were deposited over the boulder layer. The entire region was later covered by the encroaching Hawthorn sea. White's interpretation was supported by a number of later workers (Puri et al., 1967), although others have presented evidence that this hypothesis is not acceptable (Auffenberg et al., 1964).

In a 1948 review of the locality, Dr. A. S. Romer of the MCZ summarized all previously presented interpretations concerning the mode of deposition of the Thomas Farm locality (Romer, 1948), and expressed support for the fluvial hypothesis. He also reported the depth of unexcavated fossiliferous sediments exceeded 40 feet and in area approached an acre. This information was evidently obtained by analsyis of augers or cores, presumably those taken by C. Simpson in 1941.

In 1956, Dr. Robert Bader of the UF Department of Zoology, who participated in the Thomas Farm excavation for several years, reviewed the hypotheses concerning the locality in his paper on Thomas Farm equids (Bader, 1956). Bader favored the sinkhole interpretation, and also suggested that the sinkhole had been stream fed. He rejected White's identification of the uppermost sand layer as the Hawthorne Formation, and contended that the area had not been covered by the Miocene sea.

The years 1955 through 1957 were very active field seasons for the MCZ and the FGS. During that period, a permanent topographic map of the site was constructed based on a nearby USGS benchmark, and a number of auger samples were taken and analyzed by FGS geologists. Photographs taken by Dr. Bryan Patterson of the MCZ show the locations of major excavation trenches (Figure 3-2). Several of these trenches have been relocated in recent work at the site. The findings of the FGS are discussed below.

Mr. Stanley J. Olsen, originally of Harvard, joined the Florida Geological Survey in 1956. He expanded Bader's (1956) view of site formation into a more elaborate interpretation of the mode of

deposition of the Thomas Farm, describing the site as a combination sinkhole-stream-cave complex (Olsen, 1959, 1962). This interpretation was apparently based more heavily on the types of animals known to occur at the locality than on sedimentological evidence. Dr. Walter Auffenberg of the FSM (1963a, 1963b), who agreed with Olsen's views, published an educational booklet containing an illustrated reconstruction of the site. Dr. Richard Estes (1963) described the salamander and lizard component of the herpetofauna, and suggested, without first-hand knowledge of the site, that deposition had taken place in spring-fed, seasonally water-filled sinkhole.

Two FGS publications released in the 1960s (Puri and Vernon, 1964; Puri, Yon and Oglesby 1967) contained maps and stratigraphic descriptions of the Thomas Farm locality prepared principally by S. J. Olsen. I have used this map in the present study. Puri et al. (1964, 1967) cited several sedimentological features of the site that they interpreted as evidence of fluvial deposition. They listed three major sediment facies of the locality: an aquatic blue-green clay, the boulder layer, and crossbedded lime sands. Their published description of the mode of deposition is very similar to that proposed by White (1942a). In addition, based on the presence of bat fossils at the locality, they suggested that the stream was directly associated with a sinkhole or a cavern.

From the late 1950s through the 1960s, fieldwork at the Thomas Farm was conducted sporadically. The site was cleared in preparation for the 1964 Society of Vertebrate Paleontology field trip. The Field Trip Guidebook published for the meeting (Auffenberg, et al., 1964) discussed the major sedimentary and faunal characteristics of the

Thomas Farm and reviewed the hypotheses of site formation. Dr. Thomas Patton of the FSM, who provided much of the material for the Guidebook, began collecting at the site during the mid 1960s.

In the summers of 1971 through 1973, Dr. Walter Auffenberg and an FSM crew spent several weeks in the field at the Thomas Farm locality. Notes taken by Dr. Auffenberg and David Frailey in the 1973 field season show the location of their dig for that year. Auffenberg and Frailey used the limestone outcrop in the northwestern edge of the site as a reference point for the northwestern stake of a grid system, and a point 30 feet due south of the old northern gatepost as the northeastern stake. The grid was composed of 10-foot by 10-foot squares designated by the letters A through F from west to east, and by the numbers 1-5 from north to south. It is unclear whether the grid possessed 6 or 7 west-east squares. The map of the grid in the notes lists only 6 (A thorugh F), however, the distance between the northwestern and northeastern corners of the grid exceeds 70 feet, indicating either an error of over 10 feet was made in measuring, or that the grid system actually contained seven east-west squares.

Although the grid measurements obtained from the field notes are not exact, the approximate location of the 1973 grid and excavation is shown on a map of the site (Figure 3-1). Several of Auffenberg's trenches have been relocated in the most recent excavation, although none of the stakes were found in place. Sediment levels in Auffenberg's dig were designated by i, ii, and iii from highest to lowest levels. The criteria used to identify these levels are not stated in the field notes, and so far I have not been able to correlate the three levels with actual sediment units within the site.

From the middle to late 1970s and into the early 1980s FSM field efforts were concentrated on the late Miocene Love Site in Archer, Florida, and trips to the Thomas Farm were made infrequently. In 1980, Thomas Farm was extensively cleared for the 40th annual Society of Vertebrate Paleontolgy field trip (Webb and MacFadden, 1980). Excavation for the current study began in 1981 and continued on a regular basis through 1984.

In the course of the most recent excavation, I employed the digging and collecting techniques described in Chapter 2. Information obtained on the sediments excavated was used to construct a detailed stratigraphic section. This section is shown in Figure 3-3. The recent field work has brought to light a number of features which must be explained if a reasonable interpretation of the environment of deposition is to be presented. A number of these features are related to the geology of the locality, while others pertain to faunal characteristics of the site. The findings concerning the geology will be discussed in this chapter in an attempt to present a viable hypothesis concerning the mode of formation of the Thomas Farm locality. Results of faunal analysis will be considered more extensively in following chapters.

Geology

The geology of the Thomas Farm locality is complex and is further complicated by that fact that portions of sedimentary layers have been removed in previous excavations. The composite stratigraphic section of the site (Figure 3-3) shows a number of features relevant to the following discussion. Among these features, the following warrant detailed consideration:

1. Sedimentary layers dip south-southwest.
2. Extensive boulder layers of the upper member of the Crystal River Formation and the Suwannee Limestone are found in the central portion of the site. Neither of these two limestone units are found in place today within 25 miles of the locality.
3. The lower sediments are sequences of clay and sand layers. They are rich in large vertebrates, but microvertebrates are rare.
4. The upper boulder layer is overlain by massive beds of lime-sand rich in microvertebrates. Large vertebrate remains are rare in these layers.

1. Dip of Beds

One of the most obvious features of the Thomas Farm sediments is that the beds exhibit a pronounced dip to the south-southwest. The beds strike from 255 degrees east of North to 310 degrees east of North, with the majority striking almost due west. Dips of the various beds average from 12 degrees to 22 degrees to the south-southwest. Although this feature may be clearly seen in White's stratigraphic reconstruction of the deposit (White, 1942a:Plate 14), and in photographs taken during the 1956 field season (Figure 3-2), only the 1964 SVP Guidebook (Auffenberg et al., 1964) makes reference to this characteristic.

Table 3-1 lists the mean strikes and dips recorded for the various levels excavated. Two major dip directions are evident. The lower layers dip southwest at about 220 degrees east of North. A change in dip direction occurs in the upper part of the massive sand

layer designated as unit 5. Upper unit 5 and higher layers dip to 180 degrees East of North. The degree of dip is steeper in the upper layers. Since there is no evidence of substantial regional dips in north-central Florida, the presence of dipping beds requires explanation.

One hypothesis, involving tilting by post-depositional tectonic activity, is quite unlikely for a number of reasons. Such phenomena are rare in Florida's geological history. In addition, evidence for subsidence would be provided by excessive faulting over an extensive area. There are small faults in several regions of the site, but they appear to be associated with local post-depositional compaction and are hardly part of a regional pattern. The fact that there are two different sets of bed orientations within the site also indicates that these are local intraformational structural features.

The alternative explanation is that the dip of the beds reflects their original position at the time of deposition. Acceptance of this hypothesis limits the number of geologic conditions under which the fossiliferous sediments may have formed. Deposits reflecting fluvial action do not possess sets of beds that uniformly dip steeply over distances of several meters, and beds laid in standing water are ordinarily level except for slumping. The two most common non-marine geologic conditions under which beds show consistent dip are deltas and alluvial fans (Twenhofel, 1932). There is no evidence to suggest that either of these two features are represented at Thomas Farm: both require large streams or rivers, and the latter is characteristic of arid mountainous regions. A third means by which large sets of beds may be deposited on an angle is seen in regions of karst and involves

formation of a debris cone at the bottom of a sinkhole (Sweeting, 1973; Brain, 1981). If the opening to a sinkhole is relatively constricted, the sediment influx is confined to a limited area and sediment accumulates in a cone-shaped pile on the floor of the sink. The surface sediments in north-central Florida are underlain by limestone that has been subject to solution by ground water since the early Miocene (Cooke, 1945; Puri and Vernon, 1964), so it is likely that the Thomas Farm deposit represents the remains of a Miocene sinkhole. The small-scale debris cone model formed in an aquarium (see Chapter 2, p. 21) shows that sedimentation under the above described conditions does result in uniformly dipping sediment layers (Figure 3-4). The sinkhole hypothesis was one of the first put forward to explain the mode of deposition of the Thomas Farm (Simpson, 1932). This idea will be developed in detail in a discussion of several of the specific depositional features of the locality.

Figure 3-5 presents a hypothetical view of how initial roof collapse would result in a pile of boulders forming the base of the cone. This rubble pile has not yet been located in the site, but it should be found at the bottom of the deposit.

In ideal circumstances, a debris cone that forms in the center of a sink is conical in shape and exhibits a number of recognizable features. In a natural environment, perfect symmetry would not be expected, but a number of characteristics pertaining to the dip of the beds and general shape of the cone could be identified.

As one moves across the surface of a cone at any given depth, the compass direction of dip should change. This relationship is illustrated in Figure 3-6. Dip also changes more rapidly near the

apex of the cone (along line 1 in Figure 3-6) than near the base of the cone (along line 2 in Figure 3-6). Applying this model to the Thomas Farm locality, it is expected that directions of maximum dips recorded in the eastern regions of the site would be more easterly than those taken in more western sections of the site. Due to the relatively small area excavated, few sediment orientation measurements were taken in widely separated eastern and western squares. Those layers in which strikes and dips were taken at east-to-west distances of greater than 5 meters are lower 5, 7, and 8. These beds do show an easterly to westerly trend in dip directions, although there is also some local variation. The fact that the change in dip direction is slight, averaging 15 degrees along an east-west distance of 5 meters, may indicate either that most of the recent sediment measurements on excavated areas were taken near the base of the cone, or that the debris cone is extremely large if the excavated region is not near the base of the sink. Based on the amount of change in east-to-west dip directions of the various layers, the circumference of the cone taken at the level of unit 5 through 8 may be estimated:

$$\text{Circumference} = (a)\ 360 \text{ degrees}/b$$

where a is the maximum east-west distance between two dip readings, and b is the amount of change in dip, in degrees, across a. The circumference estimates of the cone in units 5, 7 and 8 range from 108 to 140 meters; therefore the mininum diameter of the sinkhole was at least 35 to 45 meters.

Figure 3-6b illustrates another characteristic of a debris cone possessing dipping beds. In heading north along a level line that passes through the central longitudinal axis of a cone from a given

point of the on the due south face, dip direction should suddenly change to the north if the cone is symmetrical. Assuming the above calculations of debris cone size are reasonably accurate, the length of line xy measured from point x on the south face of the cone in unit 7 to point y on the north face in unit 7 is 17 meters. It is unlikely that north-dipping sediments, if they exist, will ever be exposed. A pole barn and a driveway are located 17 meters north of the excavation, and the present elevation of this region is over about 15 feet higher than that of the dig.

It is possible that the debris cone did not form in the center of the sink, but that the sediments accumulated near the northern wall of the sinkhole, and thus the northern-dipping beds were truncated. The map of the locality (Figure 3-1) shows the location of a pinnacle of Middle Crystal River Limestone on the northern edge of the pit. This outcrop may be a remnant of the northern wall of the sink. Two FGS auger samples were taken to the north of the site in 1956, and one reportedly hit limestone at an elevation of 39 feet above sea level (25 feet below ground surface). However, as the type of limestone was not identified, it cannot be stated whether it was in place, or part of a rubble layer.

As noted above, there is a change in dip attitude of all beds above unit 5a (Table 3-1). Dip directions of the lower layers average 220 degrees to the southwest. Starting with the the upper layers of massive unit 5, the dips change to a more southerly (175-190 degrees east of North) orientation, and average this reading throughout the remainder of the stratigraphic sequence. The change in dip direction may be the result of a change in the location of initial sediment

input, as shown in Figure 3-7, which schematically illustrates results of laboratory experiments with the sinkhole model (Chapter 2, p. 21). An increase in the size of the opening through which sediment falls, or displacement of the position of the opening toward the west results in the formation of a second cone that partially overlies the first. Dip directions of beds forming the upper cone are shifted eastward relative to dips of beds in the lower cone. It is not unlikely that the source of sediment input at Thomas Farm may have shifted slightly to the west, either by the formation of a larger opening at the top of the sink, or by blockage of the previous opening, causing a change in the direction of dip of the beds. Presumably, enlargement of the opening would involve introduction of limestone rubble into the site; however, there is no evidence that a rubble fall occurred at the time bed dip shifted. Sediments of units 5a and 5b are very similar and both lack large boulders of limestone. The original opening may have been constricted by slippage of a large fragment of limestone that initially blocked the eastern portion of the sink entry. This huge boulder may have subsequently fallen and formed the lower boulder layer in unit 8 (Figures 3-3 and 3-8).

2. Features of the Limestone and Boulder Layers

The limestones at the Thomas Farm locality, both the in-place Paleogene limestone and that redeposited in the Miocene boulder layers, provide a great deal of information concerning the type of environment, and the mode of deposition. Although limestones of three different ages are present within the site, only the oldest is still found in place. For this reason, the height of the original limestone walls of the sink can only be estimated. A limestone outcrop is

located at the northwestern edge of the excavation (Figure 3-1). The exposed portion of the outcrop extends approximately 3 meters above the present ground surface, and contains invertebrate fossils such as the echinoid Oligopygus wetherbyi and the pecten Amusium ocalanum, index fossils of the middle member of the Crystal River Formation (Puri and Vernon, 1964; Williams et al., 1977).

Unit 8, the lower massive boulder layer within the site (Figure 3-3), is composed primarily of the upper member of the Crystal River Formation, as evidenced by presence of the annelid worm Rotularia vernoni (Nicol and Jones, 1982). This layer is thickest in the easternmost region of the excavation (over 2 meters in thickness), but pinches out toward the west. The boulders vary from completely unweathered angular fragments to weathered subangular boulders. The surrounding matrix is a fine limestone sand, although thin clay drapes are found in some regions of the boulder layer. Excavation of this level has not been extensive, and it is not clear at this point if mean boulder size changes within the layer. It appears that many of the boulders have also undergone post-depositional breakdown as the result of ground water solution. The vertebrate fossils found the boulder layer have been crushed by post-depositional compaction.

In addition to the rubble layer, two large fragments of upper Crystal River limestone have been located in the southern part of the excavation. One was encountered in the southern portion of the site in the course of excavation a north-south trench through 10N,10E and 5N,10E. It measures nearly 2 meters across, but its thickness has not yet been determined. Another huge fragment of upper Crystal River limestone was removed by backhoe in excavation of the southeastern

portion of the eastern drainage trench. This boulder exceeds 3 meters in diameter, and may have been broken off the the piece of limestone exposed in 5N,10W. It is clear that these huge fragments of limestone were once part of a wall or roof of a sinkhole (Figure 3-5), and were not transported to the locality by a stream. The limestone is not a portion of an in-place wall, as its elevation within the site is lower than top of the middle Crystal River outcrop.

The upper boulder layer, unit 11, is composed almost entirely of the friable Oligocene Suwannee Limestone, characterized by the echinoid Rhyncolampus gouldii (Puri and Vernon, 1964). This boulder layer is similar to the underlying rubble unit, except that many of the boulders are rounded and show evidence of extensive solution. Some attain great size (over 25 cm in diameter). The thickness of boulder layer thins to the west and is replaced by a layer of fine white limestone sand. Large numbers of vertebrate fossils are found in unit 11. Complete skulls are not uncommon, but they are badly crushed.

The boulder bars are separated by a layer of fine white sand, indicating that the collapse occurred as two separate events. In the eastern region of the site where boulders are thickest (Figure 3-8a) the sand layer is extremely thin, but thickens gradually toward the west. Both the boulder layers thin toward the west. This type of relationship was reproduced in the laboratory with the sinkhole model (Figure 3-8b). Boulders pile up just below the point of input but pinch out along the sides of the cone. Sandy sediments that fall on top of the boulder layer are thickest along the sides and near the base of the cone. The introduction of a second boulder layer on top

of the sand causes compaction of the sand at the point of initial input, but the sand layer remains thick on either side of the apex. This difference in the relative thickness of sand and boulder layers is due primarily to the differing angles of repose achieved by the two sediment types. The relationship of these layers corroborates other evidence of a complex debris cone within the site.

The upper member of the Crystal River Formation and the Suwannee Limestone do not occur in place today at the Thomas Farm or in the nearby region. Their absence from the area prompted White (1942a), and later Puri et al. (1967), to state that the boulders had been transported from some distance upstream by a fluvial system of high competence. The thickness of the boulder layers, coupled with the size of the boulders and limestone fragments, indicate that fluvial transport could not have been responsible for deposition of these sedimentary layers. It is more likely that during the Miocene a complete stratigraphic section of middle Crystal River through Suwannee Limestone existed at the site. The nearest measured section containing a complete sequence occurs near Mayo, where it is well-exposed in a quarry some 50 miles to the north of Thomas Farm. Judging from the thickness of this section (G. Morgan and R. Portell, pers. comm.) and of the type section in Citrus County, Florida (Puri and Vernon, 1964), the limestone walls of the sinkhole probably exceeded 30 meters in height.

3. Clay layers

The sediments found below the boulder bar are predominantly clay and sandy-clay layers. Many of these beds are composed of numerous fine laminae, indicating that the sediments were water-laid (Dunbar

and Rodgers, 1957). Vertebrate fossils of medium to large size animals are found concentrated in specific layers. Units 1 through 4 have been exposed only recently, and were not extensively excavated. Unit 5a and 5b are both laminated orange sandy-clays, made up of fine layers. The two portions of unit 5 were given separate letter designations because of the change in dip direction that occurs between them. Total thickness of unit 5 averages about 43 cm. It is overlain by unit 6, a gray clay layer with cobble to pebble size fragments of middle Crystal River Limestone. Vertebrate fossils are numerous in this portion of the unit. Unit 6 grades upward into a sandy-clay. Its thickness varies somewhat over the area excavated, ranging from 10 to 18 cm. Unit 7 is very similar to unit 6, and is composed of a clay-pebble layer that grades into a sand layer. Unit 7 is about 15 cm thick. The lowest portion of unit 8 is composed of clay-sand layers, rich in vertebrate fossils. In the upper level of unit 8, the large boulders are surrounded by fine sand.

4. Limestone Sand layers

The sediments above the boulder bar are several beds of limestone sand composed of breakdown products of the middle member of the Crystal River Formation (M. McKinney, pers. comm.). The grains are not weathered, and invertebrates characteristic of this limestone are identifiable. The layers above the upper boulder bar have been designated as units 12 through 17. Each of these beds is a massive sand layer separated from the overlying unit by a thin clay lamina or a layer of calicite. Microfauna are amazingly abundant and well-preserved in these layers, particularly in unit 15. A complete section of the layers above the boulder bar was exposed in a trench

dug through southern edge of the 5N,10E square. The total thickness of these layers is over 1.5 meters.

Site Formation

The process of limestone solution and site formation is hypothesized to have followed the sequence of events outlined in Figure 3-5. Deposition probably began when an initial collapse caused the formation of a chamber within the limestone. With the subsequent collapse of the chamber roof, a sinkhole was formed. The sinkhole is pictured here as jug-shaped, as this is a characteristic shape seen in early stages of sinkhole evolution. Early in the history of its development, the Thomas Farm sinkhole was water-filled, perhaps seasonally. The lower clay layers were water-laid and contain a higher proportion of aquatic vertebrates relative to the upper units (Chapter 4). The sinkhole was possibly fed by an underground stream or spring in the Crystal River Limestone, or by ground water seeping through fissures in middle Crystal River Limestone, as all limestone fragments found in these layers are of middle Crystal River age. The water in the sink was not stagnant, but drained to the southwest. Evidence for this observation is discussed in Chapter 4. Vertebrate bones accumulated attritionally in the sediments (see Chapter 4 and 10). Remains were either washed in from the surrounding area, or the sink may have functioned as a natural trap. Bodies of trapped animals may have floated in the water until decomposition was complete and all the bones had fallen to the floor of the sink. It is possible that bones initially accumulated on a narrow ledge in the upper portion of the sinkhole, similar to that in Warm Mineral Springs (Clausen et al., 1975). Some event, possibly partial collapse of part of the roof or

overhang, caused a change in sediment input location and a shift in dips of beds.

The first major collapse of upper Crystal River limestone evidently occurred at the lower zone of weakness between it and the middle member of the Crystal River Formation, and along the upper unconformity between the Crystal River and Suwannee Limestones (Cooke, 1945; Puri and Vernon, 1964). The huge erratics of Crystal River Limestone may also have fallen at this time, although the sequence of their fall is unknown. Shortly after the first collapse, the unsupported overhanging portion of Suwannee Limestone also broke apart and fell onto the debris cone. The reasons for collapse of the limestone are not clearly known. One causal factor was most probably lowered water table levels (Bogli, 1980). Some of the bones found in the boulder layer may have accumulated on a ledge of Suwannee Limestone and fallen into the sink when the ledge collapsed.

Massive sand layers mark the final stages of deposition of the Thomas Farm locality. The difference between these layers and the lower clay layers indicates that after the collapse of the limestone, a major change in mode of deposition occurred. The fact that large numbers of microvertebrates, in particular bats, are present in these layers, and that the sand is composed of grains of Crystal River Limestone, provide evidence that the upper sediments were outwash from a cave in the middle member of the Crystal River Formation. It is probable that caves were present in the area prior to the major collapse event, as bat remains are found even in the lowest layers of the site; however, collapse of the sides of the sinkhole provided access to a cave that was directly involved with the depositional

process. The cave was evidently frequented by (small) mammalian and avian carnivores as well as bats (Chapters 5 and 11).

The conclusion that may be drawn from the above discussion is that nearly every hypothesis advanced in the past concerning the mode of formation of the Thomas Farm is at least partially correct. I suggest that the site was formed by sequence of depositional events, rather than by one or several concurrent events. The following chapters dealing with taphonomy of the vertebrate remains will provide further support for my hypothesis.

Figure 3-1. Maps of the Thomas Farm locality. a) Approximate location of the grid established by Auffenberg and Frailey in 1973. Stippled portion shows extent of excavated region; b) Location of the grid used in this study. Stippled portions show major trenches, black regions indicate areas excavated by bulldozer in May of 1985. Black triangle marks location of eastern edge of limestone pinnacle.

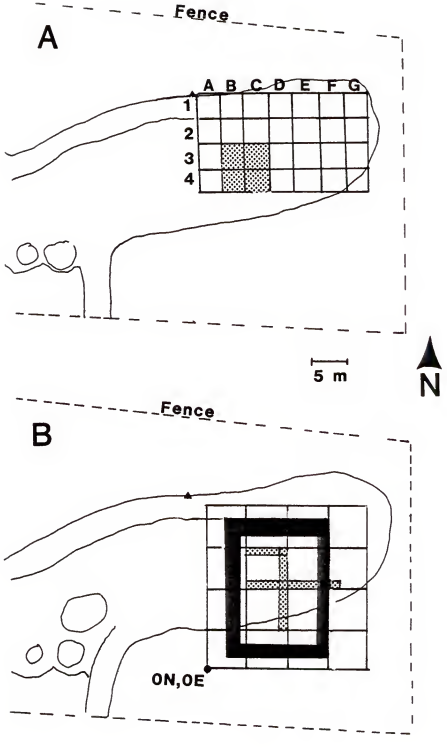
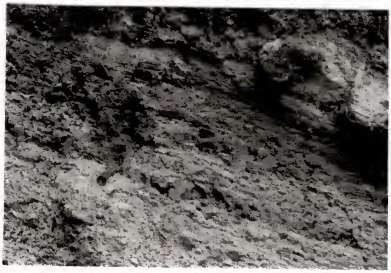

Fence
A
A B C D E F G
1
2
3
4
5 m
N
Fence
B
0N,0E

Figure 3-2. a. Photograph of the Thomas Farm excavation taken during the 1956 field season. Pictured is a trench in the northeastern region of the site. Dip of the beds to the southwest (see pick in photograph) is clearly seen. Photograph from Dr. B. Patterson's collection, courtesy of MCZ; b. Photograph of dipping beds on eastern wall of eastern trench. North indicated by black arrow.

A

B



N

Figure 3-3. Composite stratigraphic section of Thomas Farm showing the layers excavated in the most recent study. Sedimentary units are designated by numbers.

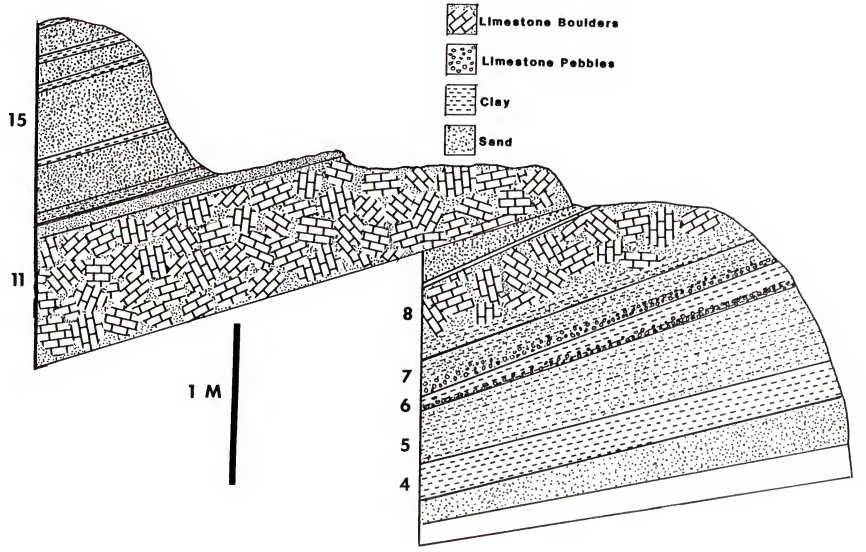

Limestone Boulders
Limestone Pebbles
Clay
Sand
15
11
8
7
6
5
4
1 M

Figure 3-4. Model debris cone constructed in the laboratory. Note dipping sediment layers.

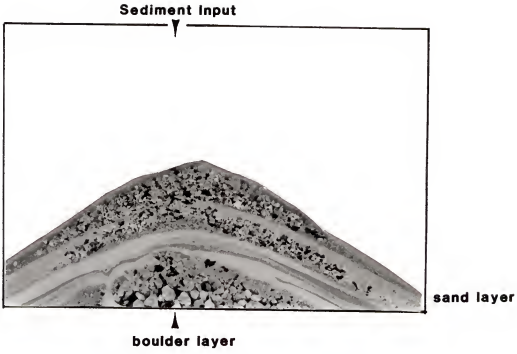

Sediment Input
sand layer
boulder layer

Figure 3-5. Schematic diagram of north-south section through a sinkhole illustrating the proposed sequence of events in the deposition of the Thomas Farm locality. a) Formation of the chamber in the limestone; b) Collapse of roof, forming sinkhole; c) Major collapse of upper Crystal River Limestone (unit 8) onto debris cone; d) Major collapse of Suwannee Limestone (unit 11) onto debris cone; e) Development of cave in vicinity of sinkhole. Abbreviations: MCR, middle Crystal River Limestone; SL, Suwannee Limestone; UCR, upper Crystal River Limestone. Wavy black lines indicate unconformities between beds. White lines indicate fissures.

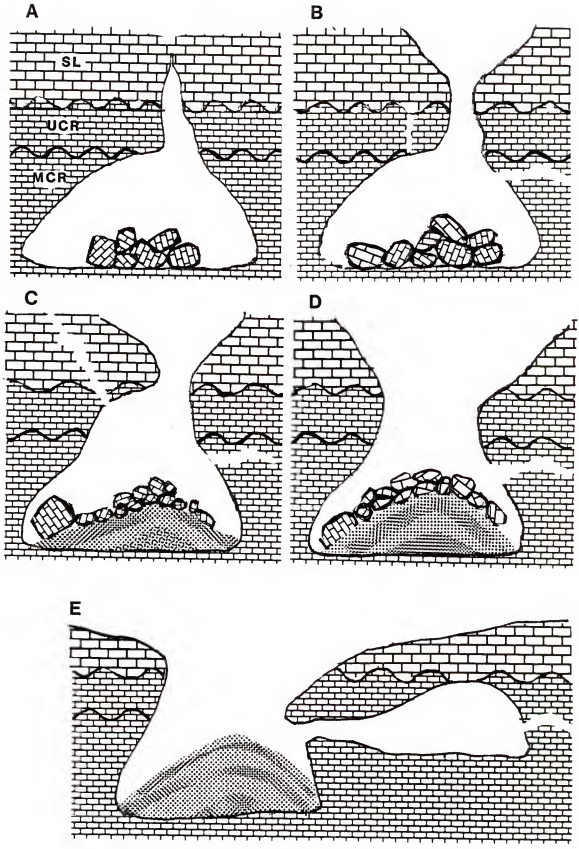
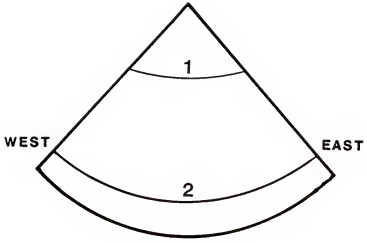

A
SL
UCR
MCR
B
C
D
E

Figure 3-6. Characteristics of sediments in a debris cone. a) Change in dip direction across the surface of a cone. Dip changes more rapidly along the smaller circumference of circle 1 near the apex than along circle 2 near the base; b) North-south longitudinal section through a debris cone showing a 180-degree change in dip direction along line xy.

A



B

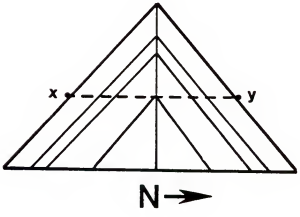


Figure 3-7. Change in dip direction on the surface of a cone caused by a change in the location of sediment input. The opening through which sediment is introduced is at point A, below which a debris cone is formed (white cone). Maximum dip of the bed through point x is 220 degrees east of North. A westerly shift in sediment input to point B results in the formation of a second cone that partially overlies the first (shaded cone). Dip taken through point x within a given layer on this second cone is 175 degrees east of North.

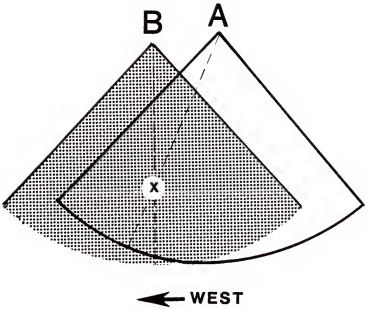
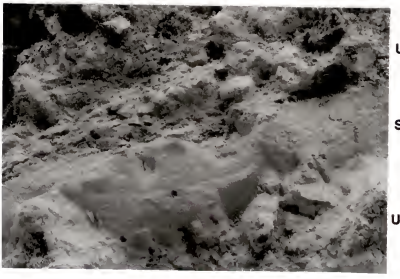
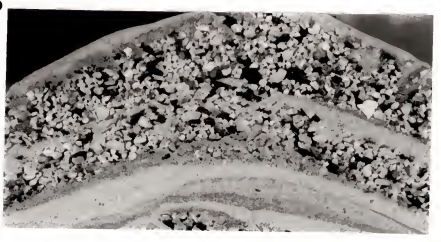

B
A
X
WEST

Figure 3-8. The relationship of sand layers to boulder layers. a) Photograph of units 8 and 11 in eastern trench. Boulders are separated by a thin layer of sand; b) Similar feature of boulder layers separated by thin sand layer in debris cone model; c) Same layers in debris cone model toward edges of cone.

A



B



C

Table 3-1. Strikes and dips taken on major sedimentary units. Abbreviations; s.d., standard deviation of mean.

Level	No. of Observations	Mean Strike degrees E of N	s.d.	Mean Dip		s.d.
1	1	314		24	SW	
2	2	314		9	SW	2.0
3	3	311	19.6	13	SW	2.6
4	2	309		13	SW	0.5
5(low)	5	312	4.8	16	SW	1.2
5(upp)	8	280	6.9	15	SW	3.1
6	1	272		22	SW	
7	12	265	9.7	21	SE	5.2
8	10	279	13.6	18	SW	4.9
9	3	261	7.3	20	SE	1.7
10	7	266	7.2	23	SE	4.8
11	4	289	32.1	14	SW	2.8
12	7	282	7.9	19	SW	3.4
14	8	281	5.2	23	SW	4.0
15	3	273	12.6	22	SW	3.7

CHAPTER 4
MEGAFAUNAL TAPHONOMY

The environment of deposition can often be inferred by analysis of the vertebrate fossils found at a locality. Factors responsible for the fossil accumulation, its faunal composition, and the condition of the fossil remains can also be ascertained. Because vertebrate fossils of all size were collected for this study, the taphonomy of the megafauna and microfauna will be covered in two separate chapters. This distinction is also methodological; most megafaunal taxa are collected by excavation in the field, whereas most microvertebrates are found by screenwashing and processing bulk matrix. There are several taxa from Thomas Farm that are considered part of megafauna because hypothetically most of their skeletal elements are large enough to be seen and recognized in the course of field excavation; however, the majority of elements of these taxa found were small and were primarily obtained by matrix picking. These "borderline groups" will be considered as both megafauna and microfauna.

The majority of taphonomic studies involve the analysis of material derived from sites that for the sake of convenience are considered to be geologically homogeneous (Wolff, 1973; Korth, 1979; Damuth, 1982; Winkler, 1983; Maas, 1985). The assumption is made that the environment of deposition is uniform throughout the site, and that the habitat sampled does not change appreciably within the locality as a whole.

The clear presence of distinct sedimentary layers within the Thomas Farm locality coupled with the fact a series of depositional changes occurred at the site (Chapter 3) indicate that in this case an assumption of sedimentary uniformity would be erroneous. A more taphonomically informative approach requires separate collection, processing, and analysis of each major stratum.

Four major components of a megafaunal assemblage can be examined to determine mode of deposition and the relevant taphonomic factors involved. The condition of the bone itself provides evidence of physical taphonomic factors such as weathering caused by subaerial exposure (Behrensmeyer, 1975, 1978; Korth, 1979; Andrews and Cook, 1985), and abrasion characteristic of fluvially transported bone (Korth, 1979; Shipman, 1981). Specific breakage patterns, puncture holes, and gnaw marks provide evidence of biotic factors such as carnivore or scavenger activity (Hill, 1980; Binford, 1981; Haynes, 1983).

Faunal diversity and relative abundances of taxa are also used to determine the most likely depositional environment, or to infer paleohabitats near the scene of fossilization. In this study, comparison of faunal components between the various bone-bearing layers will be made to determine if taphonomic, environmental, or depositional changes occurred in the course of site formation.

Bone orientation patterns are extremely useful in taphonomic analysis (Voorhies, 1969; Hunt, 1978; Saunders, 1977; Shipman, 1981; Maas, 1985). Observations on the presence of bone articulation or skeletal association as well as compass orientations of long bones and degree of their plunge within the enclosing sediment indicate rates of

burial, evidence of scavenging, and presence or absence of water-mediated transport (Voorhies, 1969; Saunders, 1977).

Bone sorting patterns can be discerned by calculating relative representations of skeletal element types found in each layer. Bones accumulated by carnivores and other biotic means often show definite patterns of representation (Hill, 1979; Brain 1981; Binford 1981). High representation of hydrodynamically similar skeletal elements may indicate the presence of moving water at a locality and also provide estimates of minimum and maximum current speeds.

In this chapter, megafaunal vertebrate remains from the extensively excavated levels 5, 6, 7, 8, 11, and 15 will be discussed. Units 9 and 10 did not contain fossiliferous remains and therefore were not extensively worked. For each unit all elements of megafaunal taxa, including those obtained in matrix picking, will be included in abundance determinations. Inclusion of these elements increases the number of specimens of these taxa in each sample, but seldom changes the MNI calculations. The four major topics listed above will be considered for each layer investigated.

Bone Destruction and Modification

The condition of a fossil bone can provide information concerning taphonomic processes and depositional environment of a fossil locality. A bone may be altered prior to its burial, or after it has been fossilized. The types of modification that occur after the animal's death and before the bone is either completely destroyed or buried are of great interest from a taphonomic standpoint. They provide documentation of events that occurred shortly after the death

of the animal. Post-depositional changes are caused by processes that affect fossilized bone.

Hill (1980) and Binford (1981) categorized types of post-mortem damage to bone. Types of destruction can also be grouped by causative taphonomic factors (Behrensmeyer, 1978; Korth, 1979; Pratt, 1979; Binford, 1981; Haynes, 1983). A bone may be destroyed by weathering if it is exposed to climatic factors prior to its burial. Behrensmeyer (1978) documented 6 stages of weathering on recent bone, ranging from stage 0 (no modification) to stage 5, with nearly complete breakdown. Bone destruction attributable to weathering effects provides evidence that the element was exposed on the ground surface before being deposited. Within a fossil locality, recovery of elements exhibiting all stages of weathering indicates that the assemblage probably formed attritionally; however, if the fossils do not appear to be weathered, an attritional assemblage cannot be ruled out. The degree of weathering is dependent on the type of climate, or even the microclimate (Behrensmeyer, 1978). Bones that lay on the ground surface prior to burial may also exhibit fine grooves and striations caused by roots and fungi, or may show evidence of trampling by ungulates (Andrews and Cook, 1985).

Water worn or abraded bones are characteristic of fluvial environments. It is not the action of the water per se that causes bone destruction, but the waterborne sand particles that wear and polish the ends and processes of skeletal elements. The degree of water wear on a bone is related to the amount of time the element is exposed to the action of sand particles. Water wear is most frequently observed on small elements that have the potential to be

carried great distances by a fluvial current. This type of bone modification is easily recognizable, but difficult to quantify. With the exception of the study by Korth (1979) on water wear of microvertebrate remains, little information exists on the amount of abrasion seen on a bone and the length of time required to produce it. For the purposes of this study the degree of water wear is assigned to three classes. Minimal wear is indicated by slight rounding of ends of bones and processes, and pitting by sand grains on the surface of the bone. Moderately water worn bone has rounded articular ends and processes, with cancellous bone visible at articular ends. The morphological features of the bone are still evident, and the bone is identifiable. Severely water worn bone has completely abraded ends and processes. Distinguishing features have essentially been obliterated.

Carnivores are the primary biotic agents of bone destruction. Several studies on types of damage done to bone by recent carnivores have been made. Hill (1980) characterized the various types of damage attributable to predators; Binford (1981), Shipman (1981), and Haynes (1983) described bone destruction by various mammalian carnivores. Many of the characteristic features are caused by a predator's teeth. Puncture marks are round holes in the bone made by canine teeth, scoring marks are longitudinal grooves in the bone made by dragging the canines along the bone surface, and depressed fractures are seen along edges of bones that have been chewed. For a more complete description of bone destruction caused by carnivores, see Hill (1980). Fischer (1981a, b, c) discussed the destruction of bone by alligators. The majority of studies dealing with destruction of bone digested by

mammalian carnivores involve elements belonging to animals in the microvertebrate size range, and will be discussed in the following chapter.

Post-depositional damage, in particular breakage, is sometimes difficult to distinguish from pre-burial damage. The most diagnostic post-depositional break, a smooth stress fracture that occurs perpendicular to the long axis of the bone (Shipman, 1981) is caused by sediment compaction. At Thomas Farm, breakage of this type is common. Bones are often completely crushed, presumably by the weight of the overlying sediments. Once these elements have been prepared and glued together, other types of destruction on the bone surface are very difficult if not impossible to discern.

Bone Modification of Fossils from Unit 5

Vertebrate fossils recovered from unit 5 may be divided into two groups: those that show characteristic water wear, and those that are unmodified. Complete elements, although not commonly found in this unit, show no signs of pre-burial destruction, and except for post-fossilization compaction breaks, are perfect. No bones from this level show signs of weathering. Bones that have been abraded in running water are common, and include long bone fragments and podials. Water wear ranges from minimal to moderate, with podials showing the highest degree of destruction. The presence of both complete bones showing little or no pre-burial alteration, and of water worn bones, indicates that elements were derived from two sources. The complete bones were introduced into the sink from the immediate vicinity, and were buried soon after, while the water worn elements may have been carried in from farther away by running water, possibly a small stream

that ran through the karst. It is also possible that the latter elements were exposed on the bottom of the sink and were subject to sand abrasion prior to their burial. The lack of severely water worn bone argues against the presence of a stream of high competence, and indicates that the bones were not transported more than a few miles.

Bone Modification of Fossils From Units 6 though 8

Units 6 and 7 and the lower clay layer of unit 8 are very similar to one another in lithology (see Chapter 3) and faunal content. Bones recovered from these beds show predominantly two types of destruction; weathering (Behrensmeyer, 1978; Korth, 1979) and water abrasion (Korth, 1979). In unit 6, weathered elements are uncommon, and no bones show evidence of climatic destruction beyond stage 1 of Behrensmeyer (1978), characterized by fine cracks running parallel to the long axis of the bone. The most notable alteration of the fossils is abrasion caused by sand grains entrained in running water. The larger bones show signs of wear at the articular ends, where the surface of the bone has been worn away to reveal the cancellous bone beneath. This feature may also often be seen on the ends of weathered bones, however, the elements in question have none of the other characteristics (dessication cracks, flaking, et cetera) associated with weathering. No evidence of bone destruction by carnivores was noted. Although carnivores regularly chew the ends of long bones, exposing cancellous portions (Binford, 1981), this process may be recognized by the jagged or uneven edges that result.

Water worn elements of the most numerous megafaunal species, Parahippus leonensis, and Archaeohippus blackbergi, are common. Roughly 66% of the podials, in particular scaphoids, lunars, and

astragali show evidence of minimal to moderate water wear. The presence of water worn bones in both unit 6 and unit 5 indicates that either the water within the sinkhole was not stagnant, or that elements were being carried to the site of deposition by moving water.

Weathered bone is more commonly found in units 7 and 8 than in units 5 or 6, although bones from these upper layers do not show evidence of extreme weathering destruction. A number of complete elements, in particular those found in unit 8, show more evidence of weathering on the side found facing upward in the deposit. Behrensmeyer (1978) noted that the surface of a bone that is exposed to the air suffers greater climatic destruction than the side resting on the ground. The number of whole bones found with the more weathered surface up may indicate that this type of destruction occurred after the bones had attained their final resting positions prior to burial. Weathering requires that the bones be exposed to air, therefore, the bottom of the sink may have been dry for an unknown period of time. Small bones and bone fragments that are weathered and also minimally water worn do not show any relationship between side found up in the field and regions of heaviest weathering damage. It is possible that these bones were exposed subaerially elsewhere before falling into the sink, or may have been transported from their original location within the sink.

The lack of severe climatic destruction of elements may be explained in several ways. Behrensmeyer (1978) stated that, within a locality, a large group of bones that exhibit the same stage of weathering indicate the prior occurence of a of a catastrophic event, provided the remains of the animals killed by this event were exposed

to the climate before being incorporated into the fossil deposit. A single subsequent depositional event, such as a flood, was required to cause more or less simultaneous burial of these elements. Recognition of the presence of such an assemblage also requires that the weathering process be advanced beyond the first stage, a requirement not met by the fossils from levels 6 through 8. The lack of heavily weathered bones within these lower levels may mean that the bones were buried rapidly, or that microclimatic conditions were not extreme enough to cause severe or rapid bone destruction (Behrensmeyer, 1978). Because most of the recognizable features of climatic weathering result from dessication of the bone, it is possible that the lack of extreme weathering effects on Thomas Farm bone indicate that the climate was moist rather than arid. More study of climatically-caused destruction of recent bone is needed.

Bone damage caused by carnivores is absent on fossils from units 7 and 8, with the exception of 2 elements of Parahippus leonensis. A puncture hole, most likely caused by a mammalian carnivore canine (Shipman, 1981; Binford 1981; Haynes, 1983) was found on a very damaged complete calcaneum from unit 7. The broken edge of a mandibular fragment from unit 8 has numerous depression fractures similar to those seen on chewed bone (Hill, 1980; Binford, 1981). The entire surfaces of both bones are pitted. It is possible that these two elements were initially derived from scat of a large mammalian carnivore, however, the lack of bones with similar modifications implies that carnivores or scavengers did not have access to the majority of bones found in these layers.

Abrasion caused by water wear is seen on a few elements from units 7 and 8. The astragalus, an element most noticably subject to fluvial abrasion, shows minimal to moderate water wear in 3 of 5 specimens in unit 7, and in 1 of 14 specimens from unit 8. The bones obtained from the upper sand and boulder layer of unit 8 are often complete, although most have been crushed by post-depositional compaction. Little evidence of pre-burial climatic or biotic destruction can be discerned on these elements.

Bone Modification of Fossils From Unit 11

In unit 11, the upper boulder layer, large numbers of complete skeletal elements, including skulls and mandibles, are found. Unfortunately, many of the elements have been crushed or deformed by post-depositional compaction such that postmortem, pre-burial damage can not be assessed. Some of the less damaged bones show weathering features equivalent to those of early stage 1 of Behrensmeyer (1978). Very little water worn bone is found in this unit. Those bones that do show evidence of water wear are very light in color, unlike the majority of darkly-colored bones found at the locality. The reason for this difference is not known. Few bones show signs of having been modified by carnivores. A complete horse innominate possesses several puncture holes probably caused by a small canid, but the rest of the bone is not damaged. A broken piece of a horse ramus has chew marks along the edge and scoring marks on the surface (Binford, 1981). The number of complete bones present in unit 11, and the rarity of elements showing results of carnivore predation indicates that predators were involved only to a very minor extent in the accumulation of the mammalian remains found in the boulder bar.

Bone Modification of Fossils From Unit 15

Unit 15 is depauperate in megafauna and possesses no complete limb bones of megafaunal taxa. Larger vertebrates are represented by long bone fragments, teeth, and footbones. As in unit 11, the few water worn bones found in unit 15 are very light in color, but the significance of this feature cannot be explained. Evidence of bone destruction by carnivores is most pronounced in this layer. A number of small bone fragments have chipped edges, a type of damage frequently caused by gnawing (Binford, 1981), and several phalanges and distal calcanea possess puncture holes almost certainly caused by small mammalian carnivores. There is evidence that the microfauna found in unit 15 is of scatological origin (Chapter 5), so it is likely that these small elements of megafaunal taxa were either discarded or ingested by a predator.

Summary of Bone Destruction Analysis

Post-mortem, pre-burial destruction of bones from Thomas Farm provides additional evidence concerning the environment at the time of deposition. Lower units 5 and 6 (and probably 1 through 4) were formed in an aquatic environment. Moving water was a feature of the environment. A stream perhaps flowed into the sinkhole, carrying some vertebrate elements with it, and there may have been a water current within the sinkhole as well. In any case, current velocity was sufficient to cause some bone abrasion. Evidence of carnivore destruction on bones from unit 15, and the presence of large numbers of complete, unabraded elements from unit 11, indicate that a change occurred in the depositional processes forming the upper layers of the site. There appears to have been less of an aquatic influence,

although the lack of extreme weathering does suggest the bones were buried not long after their initial exposure.

Faunal Composition

The species composition of a megafauna assemblage sometimes reflects the environment in which deposition occurred. Knowledge of taxa represented and of their relative abundances are both required if a reliable interpretation is to be made. Relative abundances of taxa are estimated by 2 methods (Chapter 2, p. 19): by determining the number of identifiable specimens per taxon, or by calculating the MNI per taxon (Shotwell, 1955; Voorhies, 1969; Wolff, 1973; Grayson, 1978; Damuth, 1982). Each of these methods has problems associated with its use, involving either over-estimation or under-estimation of rare taxa. Both calculations are used in this study to assess abundances of vertebrate remains from the locality. Raw abundances do not reflect the relative abundances of the living taxa (Western, 1980; Damuth, 1982). Relative abundances and their paleoecological significance will be discussed in chapter 11. In this portion of the study, the abundance values serve as a means of comparing the faunal compositions of the various sedimentary units. Table 4-1 lists relative abundances of megafaunal taxa in units 5, 6, 7, 8, 11, and 15. Values have also been converted to percentages to facilitate comparisons between the sedimentary units.

Figure 4-1 shows the relative abundances of megafaunal orders based on numbers of identifiable specimens per taxon. Among the lower units, the relative abundances of taxa in unit 5 appear different from those of units 6 through 8. Alligators have a higher relative abundance and equids a lower relative abundance in unit 5 compared to

units 6 though 8. Units 6 through 11 appear very similar in terms of relative numbers of specimens per order, while relative abundances in unit 15 are different from those of other layers. If relative numbers of specimens per order from each layer are compared statisitically with those of other layers using the R x C test of independence (Sokal and Rohlf, 1981), relative abundances in each unit, except 6 and 7, are significantly different from those in the over-lying and under-lying units at the P = 0.01 level.

If abundances in MNI per unit are compared (Figure 4-2), the differences in relative abundances of taxa between the units are mininimized. The main reason for the apparent increase in similarity of different levels if MNI rather than number of specimens per order, are used, is a function of the number of alligator teeth (which are numerous in units 5 though 7) required to indicate the presence of more than one alligator (at least 80 teeth). Use of the R x C test of independence (Sokal and Rohlf, 1981) shows that in terms of relative MNI per order of megafaunal taxa, no sedimentary unit is significantly different from the one above or below it at the P = .01 level.

The two methods for determining abundances of taxa provide apparently condradictory conclusions with regard to the megafauna found in the various sedimentary units. However, the data actually clarify some points concerning deposition and environment at the Thomas Farm. There are differences between the layers in terms of relative numbers of megafaunal specimens represented. A closer investigation of these differences will be made below. The lack of significant differences in relative MNI per taxa within the various

levels may indicate that sample sizes from each unit should be larger before the data can be compared using MNI. However, I feel the results show that the types and abundances of the megfaunal taxa available for fossilization did not change significantly in the region during the time the deposit was being formed.

Table 4-1 shows that units 5 though 8 have higher proportions of specimens of the aquatic turtle Pseudemys than do units 11 and 15. Alligator specimens (primarily teeth) are also more numerous in these lower units. In unit 11, the percentage of numbers of specimens of Parahippus leonensis is higher than in other levels. These differences reinforce the previous conclusion that the lower layers were aquatic and were characterized by standing or moving water, and the upper layers were decidedly less aquatic.

Bone Orientation

Recent experimental work has shown that fossil bones are reliable indicators of paleocurrent direction (Voorhies, 1969; Hunt, 1978; Saunders, 1977; Shipman, 1981, Maas, 1985). Current direction, and to some degree, current velocity, may be inferred by observing orientations of bones within a fossil assemblage. Orientations of the long axes of limb bones are most frequently used to indicate dominant current direction. The degree of dip of a bone within a sedimentary layer measured along the element's long axis (plunge) may also be related to paleocurrent strength and environment of deposition. In this portion of the analysis, only those elements on which orientation readings were taken will be discussed. The shape of a particular bone determines its behavior in a fluvial system, either by causing the bone to exhibit some preferred orientation relative to the direction

of the prevailing current, or causing the element to come to rest in some stable position that resists further transport (Voorhies, 1969). Observation and quantification of bone orientation trends within a fossil assemblage have the potential to provide much information concerning the depositional environment. Compass bearings of bones are shown graphically on mirror-image rose diagrams (Voorhies, 1969; Shipman, 1981). Bearings and plunges of bones are plotted on stereonet projections (Voorhies, 1969; Ragan, 1973; Shipman, 1981).

A fluvial system possessing a current velocity sufficient to cause movement or transport of long bones (current speeds vary depending on the size of the bones and physical characteristics of the stream; as a general rule, long bones of deer-sized mammals can become aligned at current speeds near 50 cm/second) is indicated by a rose diagram simlar to that illustrated in Figure 4-3a (Voorhies, 1969; Shipman, 1981). Long bones are positioned with their long axes parallel to the prevailing current direction, and their less dense articular ends facing downstream (Voorhies, 1969). Shorter bones, or cylindrical elements with ends of more or less uniform density, tend to be aligned perpendicular to the current. The differing fluvial behavior of various element types causes the well-documented pattern shown in Figure 4-3a. It should be remembered that this rose diagram represents a hypothetical fluvially-influenced distribution, and a variation from this pattern does not necessarily indicate that bones are not exhibiting some type of preferred orientation related to water movement. In less clear-cut circumstances, all aspects of bone position should be considered. If bone orientation has been influenced by a non-random factor, then the distribution of bone

orientation directions should be significantly different from a distribution in which no preferred orientation pattern is evident (Shipman, 1981). The presence of a non-uniform orientation pattern can be determined by use of the Chi-square goodness of fit test (Sokal and Rohlf, 1981).

Bone Orientation Patterns of Entire Locality

In the assessment of fossil bone orientations at the Thomas Farm locality, a number of features of the site must be considered. Since the deposit consist of several separate fossiliferous levels, the overall orientation of bones within the entire site may obscure rather than elucidate paleocurrent direction. A rose diagram showing bearings of 913 bones with complete orientation data (Figure 4-4), does not ressemble that of a fluvial environment (Figure 4-3a), although the majority of bones (62%) are aligned in a northeast-southwest direction. This pattern is not significantly different ($P = 0.01$) from that expected if the bones were distributed uniformly (Chi-square = 9.24 at 17 d.f.). In some environments, conditions do exist in which bones appear to show no preferred orientation. Saunders (1977) showed that the pattern of orientation of bones surrounding a spring-head is not significantly different from a uniform distribution. Sedimentary evidence provided by the dip of the beds at Thomas Farm indicates that bones sampled at this locality were not concentrated around an out-flowing springhead.

If bone plunge as well as bearing is considered, a stereonet may be constructed in which each bone is indicated by a point whose coordinates are bearing direction and degree of plunge (Voorhies, 1969; Shipman, 1981). Figure 4-5 shows the stereonet of bearings and

plunges for all elements (n = 516). The predominance of points in the southwest quadrant is related not to actual bone plunge direction, but to the dip of the sediments, which obscure the plunge of the bone relative to the bed. In order to determine the true plunge of the bone relative to the sediment layer, its degree of plunge must be corrected for the dip of the bed in which it is found (Shipman, 1981:78). Once this step is accomplished, a stereonet constructed using the corrected values shows that a number of bones actually plunge northeast (Figure 4-6). This pattern is unlike that seen in a fluvial deposit (Voorhies, 1969). Voorhies suggested that in a fluvial environment, the majority of bones will behave like rocks or boulders by imbricating and dipping upstream. No such trend is seen at Thomas Farm. Significantly greater numbers of bones plunge either northeast or southwest as opposed to northwest or southeast, but there is no significant difference in the numbers of bones plunging northeast as opposed to southwest (P = 0.01).

Elimination from the rose diagram and stereonet of elements shown experimentally (Voorhies, 1969; Korth, 1979: Pratt, 1979) to have preferred orientations in directions other than parallel to the prevailing current (scapulae, carpals, phalanges, pelves, patellae, tarsals, vertebrae) results in the rose diagram and stereonet shown respectively in Figures 4-4b and 4-7. The northeast-southwest trend on the rose diagram is even more prounounced, with over 70% of the elements having their long axes aligned with this compass direction; however, the orientation pattern is not significantly different from a uniform, non-preferred orientation distribution (Chi-square = 8.7 at 17 d.f.). The stereonet of long bone bearings and plunges corrected

for the dip of the beds shows that the majority of the bones plunge northeast or southwest, but that there is no significant difference in the numbers of bones plunging northeast as opposed to southwest (Chi-square = 1.18 at 1 d.f).

Treating the Thomas Farm site as homogeneous deposit leads to the conclusion that the bones do not show a significant orientation pattern, although the majority of limb elements bear northeast-southwest. If each major sedimentary unit is considered separately, more clearcut orientation patterns emerge.

Bone Orientation Patterns in Unit 5

Fossils on which orientation measurements were taken are not very numerous in unit 5 (n = 99). The most commonly found element for which orientation data were recorded are alligator osteoderms. The rose diagram of all bone bearings in unit 5 (Figure 4-8a) shows a northeast-southwest trend in orientations. The greatest numbers of bones are aligned from from 40/220 to 70/250 degrees east of North, with over 30% of the bones located within this 30 degree span. The distribution of bone directions in Unit 5 is significantly different from uniform at the P = 0.01 level, but not the P = 0.001 level.

The sample size of limb bones only in unit 5 is too small to test for evidence of preferred bearing direction (n = 22). Over 25% of the elements are oriented with their long axes pointing 70/260 degrees east of North (Figure 4-9a), suggesting that some factor was causing alignment of the long bones along this compass direction.

Bone Orientation Patterns In Unit 6

Unit 6 is an extremely fossiliferous grey/orange pebbly clay that was excavated extensively. Figure 4-8b shows the rose diagram for 195

bone bearings from unit 6. There appears to be a strong directional trend from 10/190 to 40/220 degrees east of North, but the pattern is not significantly different from a non-preferred orientation pattern. A pronounced orientation trend emerges if long bones only are used (Figure 4-9b). Most of these elements are oriented from 10/190 to 40/220 degrees east of North, with a smaller peak seen at 100/280 to 120/300 degrees. The shape of the rose diagram has some to that of a fluvial or current-influenced environment. Long bone orientations are significantly different from uniform at the .001 level (Chi-square = 59.47 at 17 d.f.).

Bone Orientation Patterns in Unit 7

Unit 7 bone orientations are similar to those of unit 6, although the spread of preferred orientation directions is wider. The orientation patterns of all bones (Figure 4-8c) and long bones only (Figure 4-9c) are both significantly different from those expected in a uniform array. It is evident that factors responsible for bone alignment did not change dramatically between units 6 and 7.

Bone Orientation Patterns in Unit 8

In unit 8, the skeletal element orientations are not as clearly defined as in the lower two layers. The more diffuse pattern seen in Figure 4-8d is probably related the fact that unit 8 is not a uniform layer sedimentologically. The orientations of all bones in unit 8 are not significantly different from those seen in a uniform distribution (14.58 at 17 d.f.) The distributions of long bones (n = 72), shown in Figure 4-9d do show a statistically significant orientation pattern (Chi-square = 45.7 at 17 d.f.). Although the range of bone direction

is not as obvious as that of unit 6 or 7, the majority of long bones (73%) are oriented to the northeast-southwest.

Bone Orientation Patterns in Units 11 and 15

The upper massive boulder layer, Unit 11, is rich in fossil vertebrates. The general orientation pattern seen in the rose diagram in Figure 4-8e has a different preferred direction from the lower layers, with the majority of bones aligned between 40/220 and 100/280 degrees east of North. The bone orientations are not significantly different from those expected if the bones did not show a preferred orientation. If long bones only (n = 96) are plotted, (Figure 4-9e) the dominant preferred orientation is between 40/220 and 80/260 degrees east of North. However, the orientation pattern is not significantly different from uniform at the 0.01 level (Chi-square = 32.3 at 17 d.f.). No rose diagrams have been plotted for unit 15, as the number of bones collected with complete orientation data was very low (N = 8).

Significance of Bone Orientation Patterns in Units 5 Through 11

The rose diagrams showing the orientations of bones within each separate level strongly indicate that some factor caused bone alignment along a northeast-southwest axis between between 40/220 and 80/260 degrees east of North. Although none of the rose diagrams are similar to those indicating fluvial deposition (Voorhies, 1969; Maas, 1985), it is probable that moving water caused the bone orientation patterns. Evidence against the possibility that bone orientation simply indicates sheetwash in the downslope direction is provided by the fact that relatively few bone orientations were recorded in the (downdip) southeast quadrant. Water flowing down the dip of the beds

would be expected to cause bone alignment in the direction of maximum sediment dip (Figure 4-3b). In addition, it is unlikely, given that long bone orientation patterns are significantly different from a uniform distribution, that deposition occurred in standing water. The slight differences in preferred orientation direction of bones between the various levels may indicate that the prevailing current direction varied slightly throughout the course of site formation. A wide spread of bone orientations within a sedimentary unit probably indicates that the current velocity was not sufficient to cause strong alignment patterns of bones, while a narrow range may indicate current velocities sufficient to cause bone alignment.

The compass bearing of a skeletal element provides limited information concerning possible current direction and environment of deposition. To accurately determine the speed and direction of paleocurrent flow, a bone's specific behavior as a paleocurrent indicator must be examined. Much experimental work is needed in order to document the hydraulic behavior of skeletal elements in a variety of aquatic situations.

Orientations of Specific Skeletal Elements

Voorhies (1969) observed as a general rule that the larger end of a long bone tends to orient in the downstream direction. My experimental studies (Pratt, 1979), indicate that it is not necessarily the larger end that points downcurrent, but the less dense (frequently air-filled) end that is moved into the downstream position. This finding is particularly true of long bones that have been exposed to weathering.

Skeletal elements may be separated into groups according to their usefulness as paleocurrent indicators. Three categories of bones are recognized in this study;

1. Bones that show a preferred axis of orientation, and usually possess one end that repeatedly orients downcurrent. Elongate limb elements are included in this group.

2. Bones of complex shape with no obvious long axis. These elements may not show any preferred direction of orientation, but have recognizable stable resting positions in running water. Included in this group are the scapula, pelvis, and some tarsal elements.

3. Bones that do not show any preferred orientations. Most of the elements in this group are small, and not elongated in any one dimension. Podials and distal phalanges are included in group 3.

Orientation Behavior of Group 1 Elements

Most long bones, particularly limb elements, tend to orient with their long axes parallel to the direction of running water (Voorhies, 1969; Hanson, 1980). Some bones may also orient at right angles to the current. The long bones from the locality will be discussed, and their recorded positions in the field will be compared with those observed for recent bones in experimental and natural fluvial environments. All elements of one type will be considered in a group, as the numbers of any one type of element recovered from a single sedimentary unit are too small to provide useful information.

Humerus. Long axes of humeri (n = 46) clearly align with the predominant preferred direction (Figure 4-10a). The majority of

these elements are found lying between 40/220 and 80/260 degrees east of North. The directional distribution of humeri is non-uniform (Chi-square = 40.83 at 17 d.f.) at the P= 0.01 level.

The directions that the ends of the humeri point may be assessed by examining complete fossil humeri. Of thirteen humeri, 2 were found with the proximal end pointing northeast, 5 with the proximal southeast, 5 with proximal southwest, and 1 with proximal northwest. Aprroximately 77% (10/13) of the humeri were oriented in the downslope direction. Voorhies' flume experiments (1969) showed that the "larger" (interpreted here as proximal) ends of humeri of sheep, coyotes, and badgers oriented downstream in about 85% of the runs. In flume experiments on rabbit to raccoon-sized skeletal elements (Pratt, 1979), proximal ends of humeri oriented downstream about 65% of the time (37/56 trials). Experiments on behavior of fresh and weathered deer humeri in a small stream showed that the humeri were carried, and came to rest, with the proximal ends facing downstream in 5 of 5 trials. Humeri of recent deer dropped from a horizontal position into standing water fell with the denser distal end first (provided both epiphyses were present). If the proximal end was air-filled, as was observed in several trials, the humerus floated at the surface with the proximal end up. One humerus remained floating in this position for over twenty hours. The lighter end often leads the way if the element is transported downstream.

Distal portions of humeri are the most abundant parts of this element found at the Thomas Farm. Little experimental work has been conducted on orientation patterns of broken skeletal elements, although Boaz and Behrensmeyer (1976) recorded the final orientation

of a hominid distal humerus in a flume as distal downstream. Of the 25 distal humeri in the fossil deposit, 14 (56%) are oriented with the distal end pointing to the southwest, indicating that distal humeri exhibit a preferred orientation, possibly in the downcurrent direction. More experimental work is needed to confirm the accuracy of this statement.

The positions in which the humeri are found in the field also indicate that certain orientations are more stable than others. Complete humeri are most often found medial or posterior side up, while distal portions only are most frequently found posterior side up.

Radius. The orientations of 35 fossil radii are shown in the rose diagram in Figure 4-10b. Although this element is too poorly represented at Thomas Farm to be of use in statistical determination of a preferred current direction, almost 80% (28) of the radii point either northeast or southwest, documenting the bone's tendency to be aligned parallel to the prevailing current direction.

The differences in size and density of the two ends of the radius are not as pronounced as are those of the humerus, however, 5 of 8 (63%) complete radii were found with the distal end pointing southwest. Voorhies (1969) found that the larger ends (he did not specify the end, it is assumed that he meant the distal end) of sheep and coyote radii oriented downstream 72% of the time. Flume experiments on radii of small mammals (Pratt, 1979), showed no preferred end orientation for this element. Recent deer radii dropped from a horizontal position into standing water fell with the proximal end first, but the distal end did not float.

Broken proximal and distal ends of fossil radii do not show a clear pattern of end orientation, and little information can be drawn from these data. The majority of radii are oriented either with the anterior or posterior surface up. This position is to be expected, particularly for Parahippus radii, which are compressed in the anterior-posterior plane.

Femur. Few femora were collected on which orientation data could be taken (n = 27), and it is not possible to conduct a Chi-square test to determine if their arrangement, shown in Figure 4-10c, is significantly different from that expected in a uniform distribution. Roughly 33% of the femora are aligned within the 40/220 to 60/240 degree range of bearings.

Of 11 whole femora, 6 were found in the field with the distal end facing southwest, 2 with the distal northeast, 1 with the distal end southeast, and 3 with the distal northwest. Voorhies (1969) showed that the larger (it is assumed he meant distal) end of the femur oriented downstream in 78% of the flume runs. Femora of smaller mammals were also found aligned with the distal end facing downcurrent in 72% of the runs (Pratt, 1979). Recent deer femora usually possess distal ends that are lighter than the proximal ends, and although both ends may initially float, the proximal end invariably becomes waterlogged first. In one experiment, a deer femur was placed in water. The proximal end sank immediately, but the distal end remained floating for five hours. In a natural fluvial environment, a weathered femur was transported, bobbing along the water surface, until the distal end became waterlogged. In all trials conducted, the distal end faced downstream after the bone came to rest.

The proximal and distal femur portions are not abundant enough to indicate any clearcut trends in orientation, although the majority of incomplete elements were recovered with the broken end pointing toward the southwest. Experiments in the laboratory using distal femora showed that the broken end oriented downcurrent in 66% of the trials.

The preferred resting orientation of a complete femur is posterior surface up. A total of 6 complete femora were found in this position, and 3 were found anterior surface up. Proximal femora were most frequently found posterior side up, while distal femora were recovered with the medial side up in most instances.

Tibia. The orientation of fossil tibiae from the Thomas Farm (n = 62) is significantly different from uniform at the P= 0.001 level (Chi-square = 57.38 at 17 d.f.). The rose diagram of tibia orientations (Figure 4-10d) shows the preferred axis of orientation at 40/220 to 70/250 degrees east of North, similar to that of the other limb bones discussed above. Voorhies (1969) noted that the orientation of the tibia was a reliable indicator of paleocurrent direction, as this element most often comes to rest with the long axis parallel to the current and the large proximal end facing downstream. In Voorhies' flume experiments, the tibia was found in this position in over 90% of the trials. Flume studies on small mammal bones (Pratt, 1979) showed that the tibia oriented with the proximal end downstream over 87% of the time. Recent deer tibia placed in a small stream resisted movement in most cases, and in other trials rolled perpendicularly to the current. An orientation of a long bone at right angles to the current most often occurs results when the water depth is not sufficient to totally immerse the bone (Voorhies, 1969).

The proximal end of the tibia, in addition to being a good deal larger than the distal end in size, may also frequently be air-filled in a naturally dried skeleton, as evidenced by studies on deer tibiae. Tibiae of adult deer, if dropped from a horizontal position, always fell through standing water distal end first. Weathered bones sometimes initially floated with the distal end down.

The tendency for the fossil tibiae from Thomas Farm to orient with the proximal end pointing predominantly in one direction is clearly seen. Of 26 complete tibiae, 20 (over 77%) were recovered with the proximal end pointing southwest, providing strong evidence that southwest was the downstream direction. No definite orientation trend is evident for the broken proximal or distal ends of the tibia.

The preferred resting orientation of the whole tibia is medial side up. Over 38% of the tibiae (10 of 26) were found in this position at Thomas Farm. The bone may also come to rest with the posterior, but rarely the anterior-lateral surface, facing upward.

Metapodial. Relatively little experimental work has been done concerning the behavior of metapodials in hydrodynamic conditions. Fossil metapodials will be discussed as two groups, the "medial" metapodials, such as metacarpal III and metatarsal III of horses, and metacarpal and metatarsal III/IV of artiodactyls, and the "lateral" metapodials of three-toed horses. Metapodials of carnivores will not included, as orientation data was taken on relatively few of these elements. Medial metapodial orientations (n = 84) are shown in Figure 4-10e. Over 30% of these bones are aligned a 20/200 to 50/230 degree wedge on the rose diagram. The orientation pattern is significantly

different from that expected in a uniform distribution at the P = 0.01 level. (Chi-square = 34.31 at 17 d.f.).

Recent deer metapodials dropped from a horizontal position into standing water showed no preferred settling orientation, presumably because both ends are similar in size and density. It is therefore not expected that this element would exhibit a preferred end orientation. Deer metapodials in a stream may roll perpendicularly to the current or be moved parallel to it. When placed in running water, these elements came to rest with the distal end facing downstream in 66% (3 of 5) of the trials. Of 35 complete medial metapodials from the Thomas Farm, 15 (43%) are oriented with the proximal end pointing southwest and 10 (28%) with the proximal end pointing the opposite direction. The remaining 10 are equally divided; 5 with proximal ends facing northwest and 5 with proximal southeast. The lack of difference in density between the two ends of a metapodial limits the usefulness of this bone as an indicator of direction of prevailing current.

If distal portions of medial metapodials only are considered, 45% (14 of 31) point distal southwest, as opposed to 25% (8) pointing northeast, and 19% (6) northwest. Proximal fragments are most often found with the the proximal end facing downslope; of 15 proximal ends, 53% (8) are directed proximal southwest, and 33% (5) proximal southeast. Incomplete metapodials appear to be more useful in determining current direction than are complete metapodials.

The majority of medial metapodials are found lying either anterior or posterior up, although occasionally one may be found on its side. The nearly circular cross-section of a metapodial increases

the likelihood that this bone will not show any preferred side-up resting position.

Lateral metapodials of three-toed horses are fairly well-represented at the Thomas Farm locality (n = 84). Most lateral metapodials have bearings between 30/210 and 40/220 degrees east of North (Figure 4-10f), although a large number of lateral metapodials are also found with their long axes lying between 60/240 and 90/270 degrees. The orientation pattern is significantly different from uniform at the P = 0.01, but not the 0.001 level (Chi-square = 33.071 at 17 d.f.). It is not possible to conduct comparative studies on these bones using Recent specimens, as these elements are absent in modern horses. Complete fossil lateral metapodials (n = 23) were recovered with proximal ends pointing equally to the northeast, southeast, and southwest. Only 2 were aligned with the proximal end pointing northwest.

No trend is seen for proximal ends, but 41% of distal fragments (9 of 22) were found with the distal end facing southwest. Lateral metapodials are almost always found lateral or medial surface up.

Orientation Behavior of Group 2 Elements

Elements from group 2 are not necessarily found with one axis consistently aligned in the direction of the prevailing current, but these bones do exhibit some type of predictable orientation in the presence of running water. This group includes mammalian scapulae, pelves, calcanea, astragali, proximal phalanges, and alligator osteoderms.

Scapula. Remains of scapulae are relatively rare at the Thomas Farm locality. There are only 13 scapulae with complete orientation

data, and their orientation does not fit any readily observable pattern.

Pelvis. Only 16 pelves found in the field at Thomas Farm were considered complete enough for data recording. Numbers of bearing readings taken on innominates are too few to show a directional trend, but 13 of the 16 innominates mapped were found with the lateral (acetabular) surface up. In flume studies on large mammals (Voorhies, 1969; Korth, 1979) transport of complete pelves joined at the pubic symphysis has been observed. Complete pelves are rare at fossil localities, so these studies are of limited use in analysis of hydraulic behavior of fossil innominates. My studies on flume transport of innominates of small mammals (Pratt, 1979) showed that innominates introduced into the flume with the medial surface up would eventually flip over and come to rest with the lateral surface up. Even under conditions of increased current velocity, these elements resisted further change in medial-lateral orientation. The majority of pelvic elements found at the Thomas Farm locality in the fluvially-stable position indicate that current velocities were sufficent to cause these elements to be moved from a less stable position and come to rest with the medial surface down.

Astragalus and calcaneum. Most astragali are cube-like in external outline, and do not show an obvious preferred directional orientation; however, 31% of the astragali found at the Thomas Farm were oriented with the proximal end facing southwest (14 of 44). The preferred resting orientation of the astragalus is with the trochlear or plantar surface up, as these sides are wider and flatter than the medial or lateral sides. Of 44 calcanea, 14 (31%) were found with the

proximal-distal axis oriented from 100/280 to 120/300 degrees east of North. The calcaneum evidently orients with its long axis perpendicular to the current direction, as well as parallel to it (see Figure 4-11a). Experiments on behavior of the calcaneum in running water show that modern horse calcanea rotate about the distal ends, usually ending with the proximal articular ends pointing downstream, while deer calcanea most often point distal downstream. The fossil calcanea from the Thomas Farm were primarily equid calcanea and showed the former trend; 29 of the 44 specimens were found with the proximal end facing in the downslope direction. The majority of calcanea were found resting either on their medial or lateral sides, rather than on the narrow anterior or posterior surfaces. The tendency of the calcaneum to orient at right angles to, as well as parallel to the current direction limits its usefulness as a paleocurrent indicator.

Proximal phalanges. Proximal phalanges are common at the Thomas Farm locality. The digit elements found at the locality are primarily proximal phalanges III of Parahippus and Archaeohippus. Their orientation pattern, as shown on the rose diagram (Figure 4-11b) possesses two peaks, one parallel to the proposed current direction at about 30/210 to 50/230 degrees east of North, and a second, less well-defined peak at about 90/270 to 120/300 degrees, oblique to the first peak. Proximal phalanges can be classified as "rollers" (Hanson, 1980), small, cylindrical objects that orient either parallel or perpendicular to the current direction. The orientation pattern for proximal phalanges from Thomas Farm is significantly different from random at the P = 0.01, but not the 0.001 level. The proximal end of a modern deer proximal phalanx is lighter than the distal end, and is

swung into the downcurrent or downstream direction by moving water. In a stream, proximal phalanges of deer and horses are readily transported and always come to rest with the proximal end facing downstream. At the Thomas Farm, proximal phalanges are oriented primarily with the proximal ends oriented downslope (28 pointing proximal southwest, 24 pointing proximal southeast), suggesting their alignment reflects a paleocurrent gradient. Although orientations of phalanges are often ignored in taphonomic studies, these elements are sometimes abundant in fossil localities, and can of some use as indicators of current direction.

Alligator osteoderms. Osteoderm bearings are measured along the central keel and no preferred pattern of directional orientation is evident (Figure 4-11c). The notable feature of the fossil osteoderms is that over 75% (47 of 63) of the specimens were found with the external surface up. Osteoderms of modern alligators dropped from a vertical position through standing water most often land with the internal surface up. In the presence of moving water, osteoderms resting on the keel are pulled over onto the flat internal surface. Once these bones have come to rest with the external surface up, they seem to resist further movement. The fact that most of, but not all, the fossil osteoderms are found in fluvially-stable positions indicate an intermittent, periodically strong current such as that caused by the rapid draining of water through an opening in the bottom of a sinkhole may have been responsible for flipping most of the osteoderms to a more stable resting position.

Orientation Behavior of Group 3 Elements

Group 3 elements, the smaller carpals and tarsals, patellae, and

other small dense bones, need not be discussed in any detail here. The majority of these bones show no significant orientation trends when placed in running water and therefore are not useful for determining the direction of paleocurrent.

Conclusion of Bone Orientation Studies

Bone alignment at the Thomas Farm locality was influenced, at least partially, by running water. Moving water evidently flowed from the northeast (40 to 80 degrees east of North) to the southwest (220 to 260 degrees east of North). As the maximum dip of the beds is 180-190 degrees east of North in most levels, it is apparent that water was not simply running down the slope of the sediment. Bone orientations, while in most cases significantly different from a uniform or no-preferred orientation distribution, are not similar to those of a classic fluvial deposit. Current direction and velocity appears to have been variable and intermittent. Drainage of water from the sinkhole was toward the southwest and may have undergone a periodic cycle. The following section on sorting patterns of skeletal elements will provide more information concerning water current strength and possible environment of deposition.

Sorting Patterns

Some important characteristics of a fossil assemblage are related to the type of elements present and their positions relative to other bones. Bone distribution within a site may indicate those biotic or abiotic factors that have affected the assemblage prior to burial. Skeletal associations or lack thereof, and relative representations of skeletal elements both serve to provide evidence of the basic types of accumulations that may be recognized. They are, as follows:

1. Catastrophic assemblages, characterized by complete or nearly complete skeletons showing high degrees of articulation (Voorhies and Thomasson, 1979). Bone destruction by weathering, abrasion, or carnivores is not common, as burial of the remains usually occurs rapidly. Accumulations of this type are rare in the fossil record.

2. Carnivore or raptor accumulations. In a bone accumulation formed by a predator, articulation of elements is rare. Representation of certain types of elements may be extremely high. Bones may show characteristic breakage or toothmark patterns, or be acid-etched if they have passed through the carnivore's digestive tract.

3. Fluvial or current-influenced assemblages. A classic fluvial deposit is characterized by an absence of articulated elements. Concentrations of bones possessing similar hydrodynamic properties are seen, and long axes of bones are aligned according to the direction of the prevailing current. Bones may be polished or rounded by sand particle abrasion. Several fossil localities that have been the subject of taphonomic studies have been shown to be formed by fluvial action (Voorhies, 1969; Dodson, 1971; Hunt 1978; Wolff, 1973; Behrensmeyer, 1975; Korth, 1979).

The above are representative types of accumulations that are caused by one predominant physical or biotic factor, and thus are easily recognizable. A clear interpretation of the mode of formation of an assemblage is often obscured by the fact that combinations of factors may have been involved.

Skeletal Articulation or Association

The first step in determining the relevant taphonomic factors involved in formation of a bone assemblage is the analysis the positions and abundances of the bones present. Figures 4-12 and 4-13 show representative maps of megafaunal elements in square meters of units 6 and 11, respectively. The bones clearly were not articulated when they were buried. It is unlikely that the sinkhole was a natural trap in the classic sense--complete bodies did not fall in and undergo rapid burial, either in dry conditions or in quiet, stagnant water.

It is difficult to determine if any of the disarticulated elements at the Thomas Farm are from the same skeleton. The most numerous bones are those of Parahippus leonensis. It is not uncommon to find several examples of the same element of one species within a fairly small area, suggesting that associations by current selection outweigh skeletal associations. Efforts to match postcranial elements of a single individual are seriously hampered by the fact that most of the bones have been crushed or broken by post-depositional compaction. Only 2 P. leonensis elements, a left femur and left tibia found close together in field, were similar enough in size that to have belonged to the same individual. Among the lower vertebrates, a contact was found between two fragments of a Geochelone pleural found several meters apart in the same layer. No other definite matches, although sought, were encountered.

It is possible for the remains of one individual to be scattered throughout several layers, particularly in attritional assemblages where bones may be introduced into the deposit from the surface at any time. The problems encountered in searching for matches between

sedimentary units are the same as those described above. No matches of bones were found between layers.

Relative Representations of Elements

The relative representations (or percentage preservations) of various types of skeletal elements may also shed some light on the means by which fossil bones were accumulated. The proportions of various skeletal elements (relative to expected numbers based on MNI) represented at a site can provide evidence that mammalian carnivores were the primary agents of bone collection (Hill, 1979; 1980; Brain, 1981; Binford 1981; Haynes, 1983). Studies by Voorhies (1969), Behrensmeyer (1975), and Dodson (1973) have shown that skeletal elements of vertebrates possess particular hydraulic properties that affect their behavior and transportability in running water. Flume and stream studies (Voorhies, 1969), Behrensmeyer (1975), Korth, (1979) and Pratt (1979), indicate that certain types of elements tend to be transported together under fluvial conditions. These "Voorhies dispersal groups" (Voorhies, 1969), as they have come to be termed, provide one means of determining if a fossil assemblage represents a fluvial accumulation, and may help to identify some characteristics of the fluvial system.

The analysis of element percentage preservation at the Thomas Farm locality was restricted to equid elements, in particular those of Parahippus leonensis. There are several reasons for this decision. Parahippus is the most abundant member of the larger (over 10 kg) mammalian fauna at the locality, and remains of Parahippus are found in all of the major units. The elements are all easily identifiable. It is difficult to assign many of the postcranial elements of

carnivores and artiodactyls to genus, such that MNI calculations for each species must be based on cranial material, and relative representations of elements cannot be determined to genus. The size range of Parahippus is small, so the effect of size variation in transport of a particular element type need not be considered.

The relative representation of each major element type of Parahippus found in each layer was determined (Chapter 2, p. 19). Calculations of these values are shown in Table 4-2. Units 6, 7, and 8 are most similar to one another in relative representations of Parahippus elements. Numbers of elements preserved in units 5 and 15 are different from other layers. Unit 11, although similar to units 6 through 8 in bone representation, will be considered separately due to its unique lithology.

In order to obtain a large sample with which to analyze patterns, MNI and relative representation of Parahippus bones in units 6 through 8 were lumped. The calculated MNI fall from 21, if the MNI for each layer are added, to 17, if the 3 layers are treated as one. It should be kept in mind however, that the lower MNI obtained from lumping these three layers does not change the order of representation of elements from most to least abundant. The possibility that elements from one animal are represented in several different layers supports the validity of combining samples. Relative representations of Parahippus elements from the combined units 6, 7, and 8 are shown in Table 4-3.

Relative Representations of Elements Accumulated by Carnivores

Accumulations formed by large mammalian carnivores are separated into two main categories; kill sites and dens (Binford, 1981). A kill

site is the location where death of the prey takes place. Watering holes are usually classified as this type of site, as these regions are visited in large numbers by prey species, and predators often hunt there. Bony remains abandoned at a kill site are often fairly complete. In contrast, den sites contain bones that have been transported from the scene of the kill (Binford, 1981) by a predator, and in many cases have subsequently been damaged by gnawing or chewing. Bone that has been defecated is also more commonly found at a den locality than at a kill site (Binford, 1981; Andrews and Nesbit Evans, 1983).

Relative skeletal representations of artiodactyl remains from these two types of carnivore accumulations were obtained from Binford (1981), for artiodactyls ranging in size from 80 to 160 kg, and for topi, which weigh about 80 kg, close to the estimated weight of Parahippus leonensis (Hulbert, 1984). It is realized that in a comparison of a fossil assemblage with modern bone accumulations, the sample size of the recent study should be large, or the recent comparative accumulation should represent average values of a large number of studies. Unfortunately, data on modern accumulations are simply not available, so it must be kept in mind that differences between a fossil assemblage and a modern assemblage may be due in part to variations in modern assemblages. The data discussed here are based on accumulations formed by wolves, because I consider this species to be the most appropriate modern analogous species available for comparison with the Thomas Farm canids and dog-like amphicyonids.

Unit 5. Figure 4-14 shows that for unit 5, relative representations of major skeletal elements of Parahippus leonensis are

significantly different from relative representations of artiodactyls found at either a kill site or a den (R x C test of independence at P = 0.01). These results are as expected, since none of the mammalian fossils recovered from this unit show any evidence of carnivore or scavenger damage.

Unit 6-8. Percentage preservations of Parahippus elements from the combined units 6 through 8 are compared with those of artiodactyls from carnivore-accumulated assemblages (Figure 4-15). The histogram of abundances of fossil elements is very different from that of a kill site, but shows some similarity to that of a den assemblage. However, relative representations of elements from a modern carnivore den assemblage and from the fossil assemblage are significantly different from one another at the P = 0.01 level (R x C test of independence). Weathering and water abrasion, as opposed to carnivore-caused destruction, are the most frequently observed types of damage of bones from these units, and serve to reinforce the interpretation that mammalian carnivores were not a major factor in the accumulations of bones in these layers.

Unit 11. Relative representations of Parahippus elements in unit 11 bear some similarity to those of a bone assemblage at a carnivore kill site, although representations of major elements are significantly different at the P = 0.01 level (Figure 4-16). The most obvious differences between the fossil and recent accumulation are in the greater number of ilia and vertebrae found at recent sites, and the relatively greater abundance of tibia recovered from the Thomas Farm locality. These differences could be related in part to pre-depositional or post-depositional preservation biases that operate

against the the preservation of fragile elements such as vertebrae and pelves. It is also possible that hydraulic sorting modified original bone abundances. There are many scenarios that might account for bone accumulation in this unusual layer. The animals may have been killed by carnivores and their bones abandoned on a rocky talus slope by a cave, or the bones may have accumulated on a submerged ledge that later fell, forming the boulder bar. The latter interpretation is more feasible, as weathering is not a major feature of the fossils found in this layer.

The number of Parahippus specimens of unit 15 is too low to allow for analysis of percentage preservation of skeletal elements (n = 63). Remains of other large mammals (mustelid to horse size) are dominated by incisors, phalanges, podials, and vertebrae. Limb bones, with the exception of small fragments or epiphyses, are rare. The possibility that remains in this layer represent a coprocoenosis formed by small canids will be discussed in the following section.

Bone Sorting by Moving Water

Behrensmeyer (1975:491) showed that types and numbers of skeletal elements present in a fluvial assemblage are determined by paleocurrent velocity and the distance of the site of deposition from the site of initial bone transport. Hanson (1980) identified 4 basic types of bone assemblages that can form in the presence of moving water. Determining which model provides the best fit to an actual assemblage requires not only knowledge of relative representations of elements, but of their hydrodynamic properties as well. In this study, bones will be considered to have high relative representations if their abundance reflects greater than 50% of that expected.

A breakdown of the Thomas Farm Parahippus fossils from the lower layers (5, and 6-8) into Voorhies dispersal groups (Voorhies, 1969; Korth, 1979) (Tables 4-5, 4-6) shows that those elements with over 50% relative representation fall predominantly into dispersal groups II and II/III in unit 5 and I/II and II in unit 6-8 (Korth, 1979). The overall composition of sorting groups is similar in unit 5 and 6-8; I will therefore concentrate mainly on the representation of bones in the combined sample obtained for units 6 through 8. This assortment of elements may have formed in several ways. The bones present in highest numbers may be those that resisted fluvial transport from the environment while the lighter elements were removed by current winnowing. All Group I elements in units 5 and 6-8 have lower than 40% relative representation, and most (73%) are represented by less than 20% of the expected number. Groups I/II, II, and II/III are well represented (greater than 50% occurrence of elements), and Group III elements are rare. These results indicate that a current sufficient to cause transport of lighter, less dense elements removed many of the Group I bones. The low representation of Group III elements is not explained by the above scenario. Alternatively, it is possible that the assemblage of fossils represents a group of bones with similar hydrodynamic properties that were transported together to the site of deposition (type 2b model of Hanson, 1980). The heavier elements were not transported and remained upstream from the site of fossilization. A third, more complex interpretation takes into account the water worn elements, particularly the podials. It is possible that the most water worn elements were carried into the sinkhole from an unspecified distance away by a stream. A subsequent decrease in current velocity

within the sinkhole caused some of the heavier elements to be deposited on the debris cone, along with elements that fell directly into the sink from above. The lighter, Group I bones were transported from the deposition site by the reduced current.

In units 6-8, Group I and III elements are certainly underrepresented. Dentaries, which are considered lag elements, are present in greater than 50% relative abundance, but the other group III elements, the skull and maxilla, are rare (less than 40% relative representation). More intensive examination of the data must be undertaken in order to determine which of the depositional conditions described above is most acceptable.

One approach is to assume that the bones that are represented in the highest density are those that have been transported within a fairly narrow range of current velocities. Hydraulic and transport behavior may be assessed by several methods. The most useful techniques, from a paleontological standpoint, involve comparing a skeletal element to a quartz sphere for which transport velocities have been empirically determined (Allen, 1965; Behrensmeyer, 1975; Korth, 1979; Pratt, 1979). The calculation, described in Chapter 2, p. 20, provides the diameter of a quartz sphere (dq_n) based on the volume and density of the bone (Behrensmeyer, 1975).

Table 4-6 shows the quartz sphere diameters calculated for selected group I/II and II elements. Quartz grain equivalents for long bones were calculated for the most commonly represented portion of the element rather than for the whole bone; for example, tibiae and humeri found at Thomas Farm are overwhelmingly represented by distal ends only.

Within group I/II, there is little variation in quartz grain diameter. Mean grain diameter for group I/II elements is 1.8 mm based on dry densities and 2.4 mm based on wet densities. The predicted current velocity necessary to move elements in this size range is approximately 35 to 45 cm/second (Allen, 1965; Behrensmeyer, 1975). Stream transport velocities required to move modern deer and horse elements in this size range support this prediction. Most of the larger foot bones and phalanges move at very similar stream velocities. The range of quartz grain diameters, and thus expected current velocities required to cause bone transport is much wider in group II elements. Especially notable are the high quartz grain diameters of the humerus, radius and tibia, which indicate current velocities in excess of 100 cm/second were necessary to move these elements. My flume studies (Pratt, 1979), indicate that these estimates are high. I found that for elements of small mammals, small, compact elements are moved at velocities close to the predicted values, while long bones are actually transported at current velocities slower than those predicted for their nominal quartz spheres. If the same trend seen for long bones of small mammals holds for larger mammals, then the current velocities necessary to transport limb bones should be less than the predicted transport values for their quartz grain equivalents. Actual current speeds in a natural fluvial system at which modern deer humeri and tibiae were moved were close to 60 cm/second. It should also be remembered that a limb bone that has been weathered may float, or be carried readily at far lower current velocities than expected. In experiments in stream environments, naturally weathered deer humeri and femora possessing

one air-filled end were moved at current speeds sufficient to transport carpals and tarsals. Notwithstanding these observations, the fact remains that the range of predicted water velocities (from 35 to at least 60 cm/second) necessary to move the most highly represented elements in levels 6 through 8 is too great to indicate that these elements were transported as group. The interpretation of the bone assemblage as a lag group of elements that resisted transport is therefore favored. The previous discussion also indicates that the predominant current velocity was less than 35 cm/second. The third possibility mentioned previously to account for the presence of water worn bone is also acceptable. The most extensively water worn elements are astragali, cuboids, scaphoids and lunars. Less abraded elements inlcude the calcaneum and the navicular. The first four items all have very similar quartz grain equivalent diameters (mean = 2.9 mm), and it is possible that they were all carried by moving water into the sinkhole. Within the sinkhole, an intermittent current of a similar (or slightly reduced) velocity caused further transport of Group I elements.

Even if one of the hypotheses presented above is accepted, there are a number of inconsistencies between the sorting-pattern models and the actual data from the locality that should be explained. Within group I/II the various carpals and tarsals are present in abundances of less than 50%. However, the majority of these elements (71%) have relative abundances of over 40%, so they are fairly well-represented. Other elements whose underrepresentation is difficult to explain include the pelvis, scapula, and femur. The pectoral and pelvic girdle elements are bones that exhibit unpredictable hydraulic

behaviors. In addition, they are among some of the most fragile elements in the Parahippus skeleton, and it is possible that their underrepresentation is a function of some type of destruction. The femur is the only limb bone with a relative representation of less than 50%. Voorhies (1969) also found the femur to have lower than expected representations in the Verdigre deposit. He suggested that the low representation of this element was related to selective destruction by scavengers. This explanation does not account for its underrepresentation at the Thomas Farm. It is possible that the femur, by its ability to float if air-dried, may be transported from the site of deposition more readily than other long bones. The patella, which also has a lower than expected representation, also floats for long distances before becoming waterlogged.

Unit 11. The sorting pattern for Parahippus elements from unit 11 is similar to that of the lower layers (see Table 4-7) except that the disperal groups are not as obvious; there is a wider range in percent preservation ratios within one sorting group than is seen in unit 6-8. High relative representation of elements belonging to different dispersal groups indicate that fluvial influences in this layer were not as strong as in the lower layers. The degree of similarity of of bone relative representations in this layer to those of a carnivore kill site requires the comparison of the kill site with a fluvially sorted assemblage (see Table 4-9). It can clearly be seen that this type of deposit, if unmodified by other taphonomic factors, could not be mistaken for a fluvially deposited site. Elements are present in greater than 50% abundance in each of the major dispersal groups, with both elements that would be readily transported and those

that resist movement in running water being well-represented. The possibility that elements from unit 11 could be remains abandoned by carnivores need not be ruled out however. The initial bone source may have been formed in such a manner, and other factors such as water current or climatic destruction of bone may have caused the final abundance pattern seen in the fossil deposit.

Table 4-9 shows sorting groups for unit 15, based on a combined sample of Parahippus leonensis and Archaeohippus blackbergi (MNI = 3). A sample of this size presents an unreliable picture of relative representations of skeletal elements, but several points may be made concerning the megafaunal elements found in this unit. No elements have higher than 40% relative representation. The only limb bones found are the humerus and tibia, and group I elements predominate. Complete jaws, girdles and limb bones of megafaunal taxa are not found in this layer. It is possible that the bones present in unit 15 represent a transported assemblage, although they could also represent elements that were defecated by carnivores. The predominance of small taxa and juvenile individuals supports this tenative idea, which will be discussed in greater detail in the following chapter on microfauna taphonomy.

Figure 4-1. Relative abundances of orders of megafaunal taxa by number of specimens per order. a) Unit 5; b) Unit 6; c) Unit 7; d) Unit 8; e) Unit 11; f) Unit 15. Abbreviations: AR, Artiodactyla; CA, Carnivora; CH, Chelonia; CR, Crocodylia; PE, Perissodactyla. For actual values see Table 4-1.

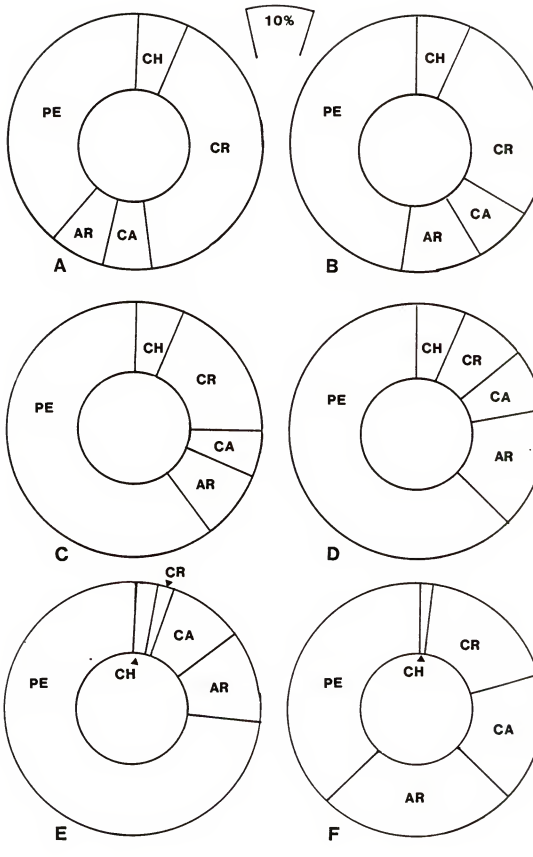

10%
CH
PE
CR
AR
CA
A
CH
PE
CR
CA
AR
B
CH
CR
PE
CA
AR
C
CH
CR
CA
PE
AR
D
CR
CA
PE
CH
AR
E
CR
PE
CH
CA
AR
F

Figure 4-2. Relative abundances of orders of megafaunal taxa by MNI. a) Unit 5; b) Unit 6; c) Unit 7; d) Unit 8; e) Unit 11; f) Unit 15. For abbreviations see Figure 4-1. For actual values see Table 4-1.

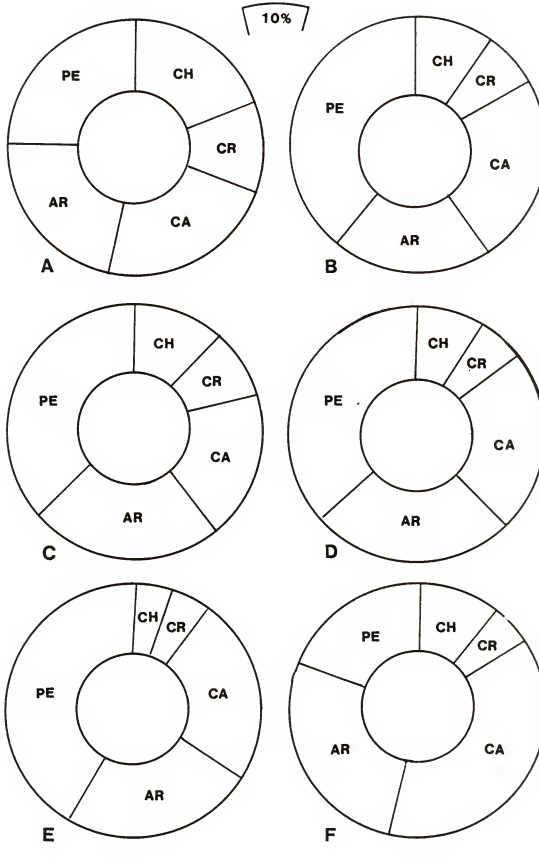

10%
PE
CH
CR
AR
CA
A
PE
CH
CR
CA
AR
B
PE
CH
CR
CA
AR
C
PE
CH
CR
CA
AR
D
PE
CH
CR
CA
AR
E
PE
CH
CR
AR
CA
F

Figure 4-3. Mirror-image rose diagram models. a) Hypothetical orientations of bones in a fluvial deposit; b) Hypothetical orientations of bones along maximum dip of bed.

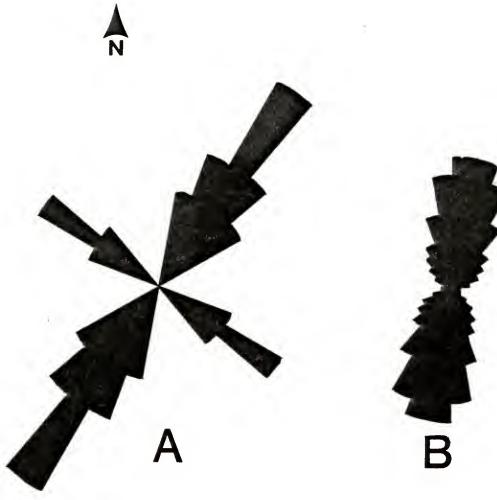

N
A
B

Figure 4-4. Mirror-image rose diagrams of bones from all sedimentary units of Thomas Farm. a) orientations of all bones with data (n = 913); b) orientations of long bones only (n = 350).

N
A
10% of bones
B

Figure 4-5. Stereonet projection of all recorded bone bearings and plunges, not corrected for dip of beds (n = 560).

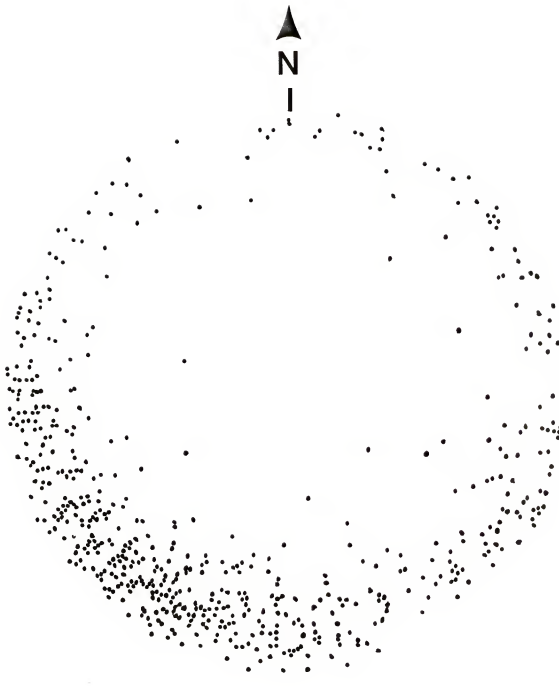

N

Figure 4-6. Stereonet projection of all recorded bone bearings and plunges, corrected for dip of the beds (n = 319).

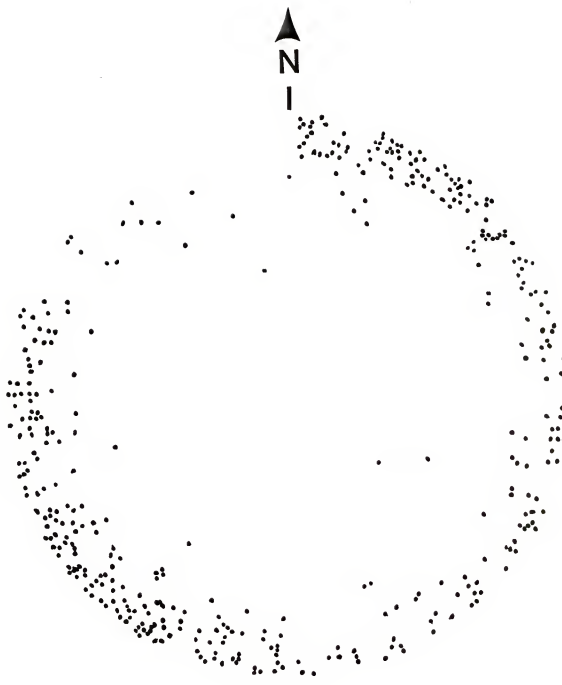

N

Figure 4-7. Stereonet projection of all recorded long bone bearings and plunges, corrected for the dip of the beds (n = 200).

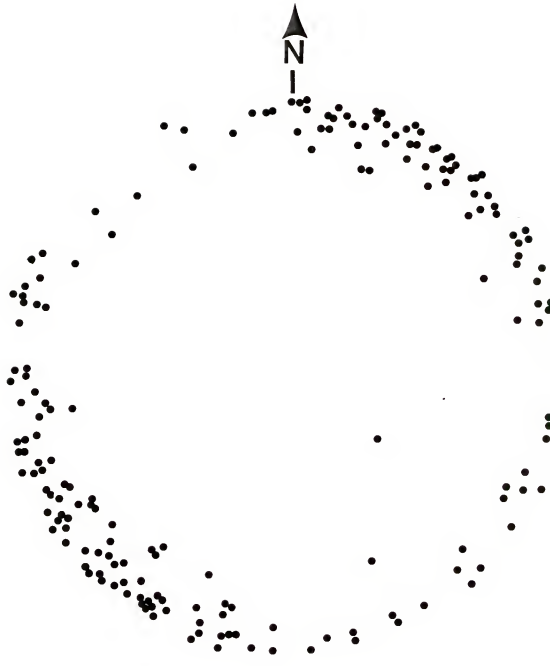

N

Figure 4-8. Mirror-image rose diagrams of bone orientations. a) Unit 5; b) Unit 6; c) Unit 7; d) Unit 8; e) Unit 11.

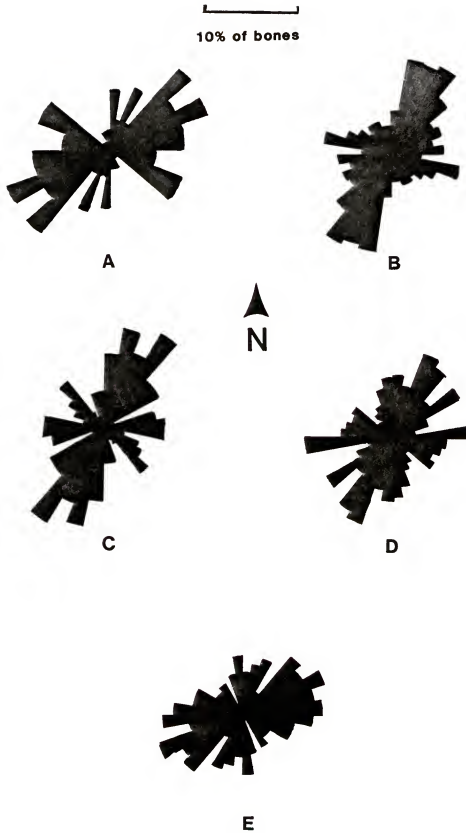

10% of bones
A
B
N
C
D
E

Figure 4-9. Mirror-image rose diagrams of long bone orientations. a) Unit 5; b) Unit 6; c) Unit 7; d) Unit 8; e) Unit 11.

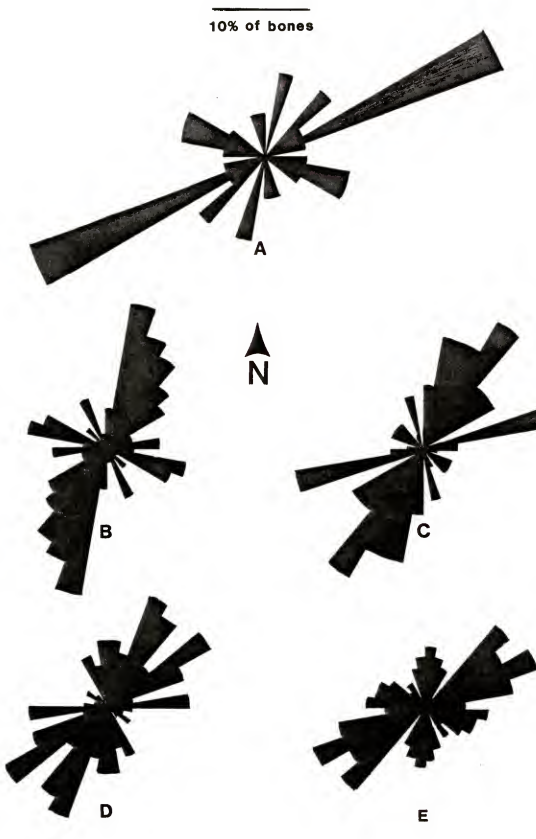

10% of bones
A
N
B
C
D
E

Figure 4-10. Mirror-image rose diagrams of orientations of selected long bones (group 1 elements). a) Humerus; b) Radius; c) Femur; d) Tibia; e) Medial metapodial f) Lateral metapodial.

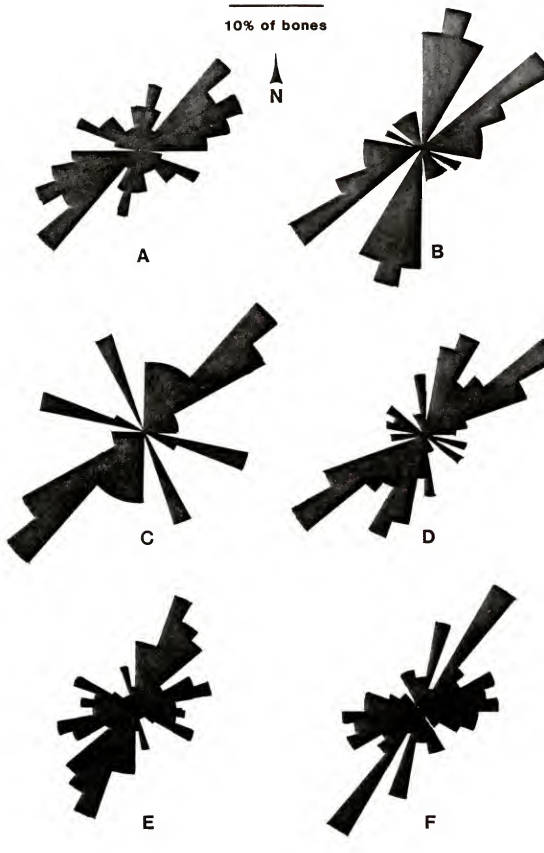

10% of bones
N
A
B
C
D
E
F

Figure 4-11. Mirror-image rose diagram of orientations of selected group 2 bones. a) Calcaneum; b) Proximal phalanx; c) Alligator osteoderm.

10% of bones

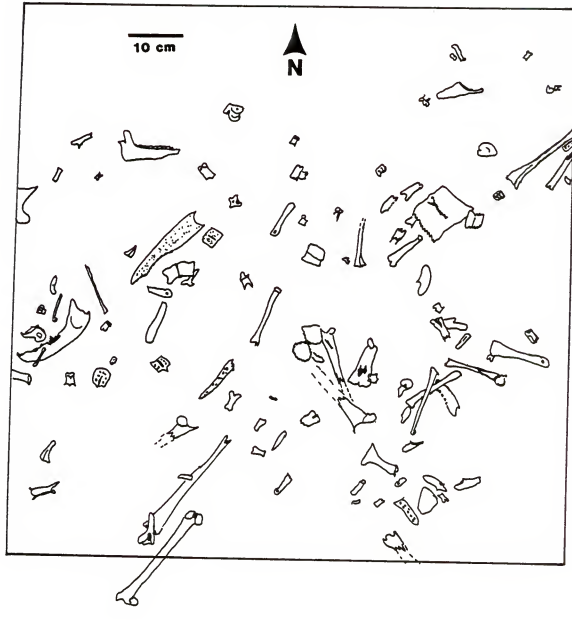
A

N

B

C

Figure 4-12. Map of representative square meter in unit 6 showing distribution of fossils.


10 cm
N

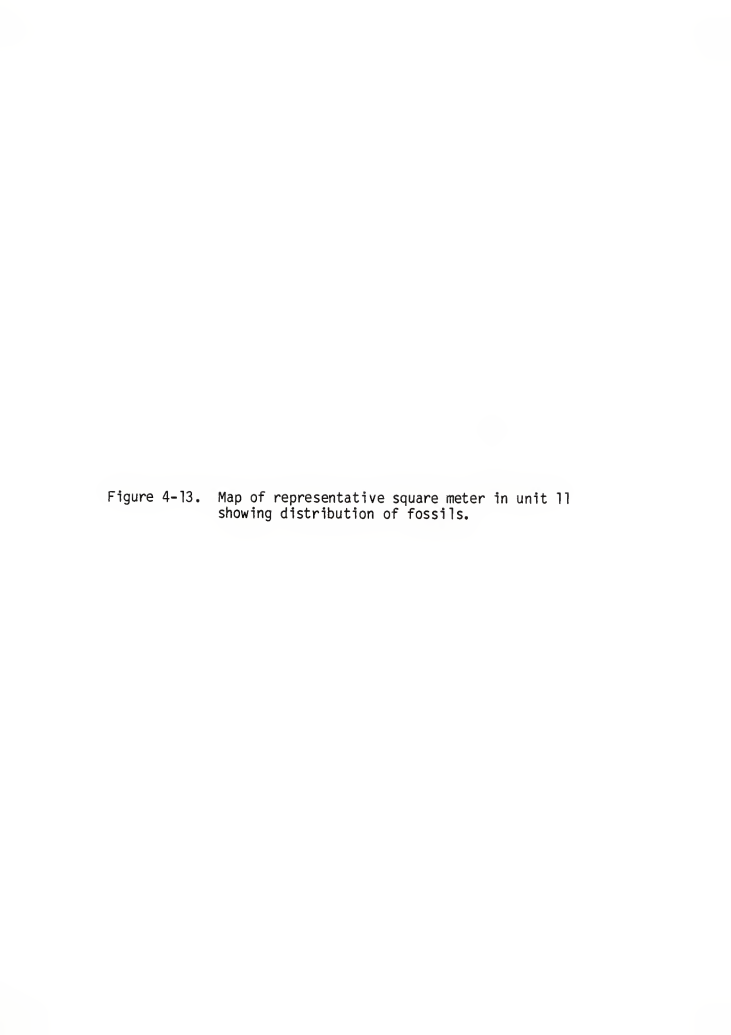


Figure 4-13. Map of representative square meter in unit 11 showing distribution of fossils.

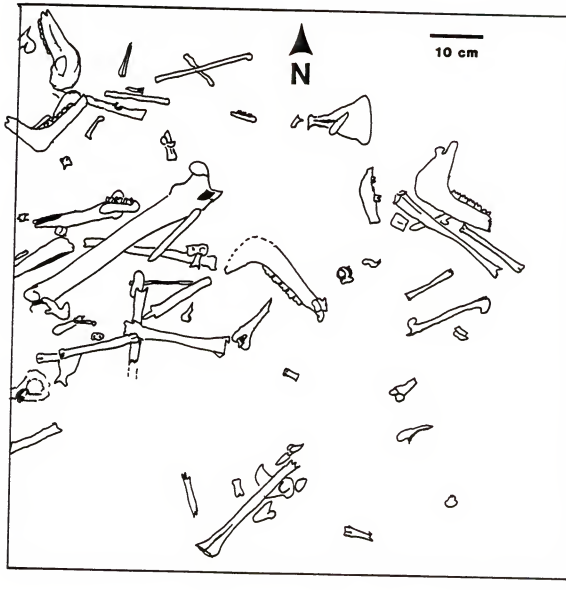

N
10 cm

Figure 4-14. Relative representations of skeletal elements in modern and fossil assemblages. a) Artiodactyl remains from a kill site (Binford, 1981); b) Artiodactyl remains from a carnivore den site (Binford, 1981); c) Parahippus remains from unit 5. Abbreviations: Ast, astragalus; Calc, calcaneum; Dent, dentary; DPh, distal phalanx; Fem, femur; Hum, humerus; Max, maxilla; Mc, metacarpal; MPh, medial phalanx; Mt, metatarsal; Pel, pelvis; PPh, proximal phalanx; Rad, radius; Rib, rib; Scap, scapula; Tib, tibia; Vert, vertebra.

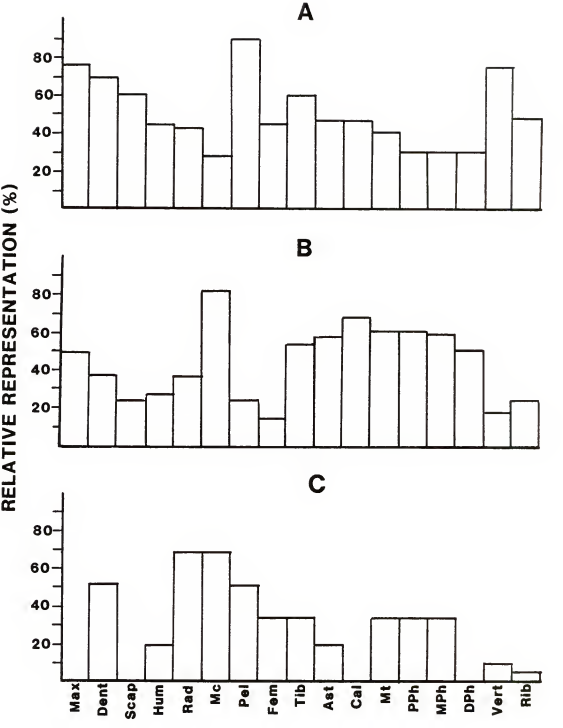

A
B
C
RELATIVE REPRESENTATION (%)
80
60
40
20
Max
Dent
Scap
Hum
Rad
Mc
Pel
Fem
Tib
Ast
Cal
Mt
PPh
MPh
DPh
Vert
Rib

Figure 4-15. Relative representations of skeletal elements in modern and fossil assemblages. a) Artiodactyl remains from a kill site (Binford, 1981); b) Artiodactyl remains from a carnivore den site (Binford, 1981); c) Parahippus remains from unit 6-8. For list of abbreviations see Figure 4-14.

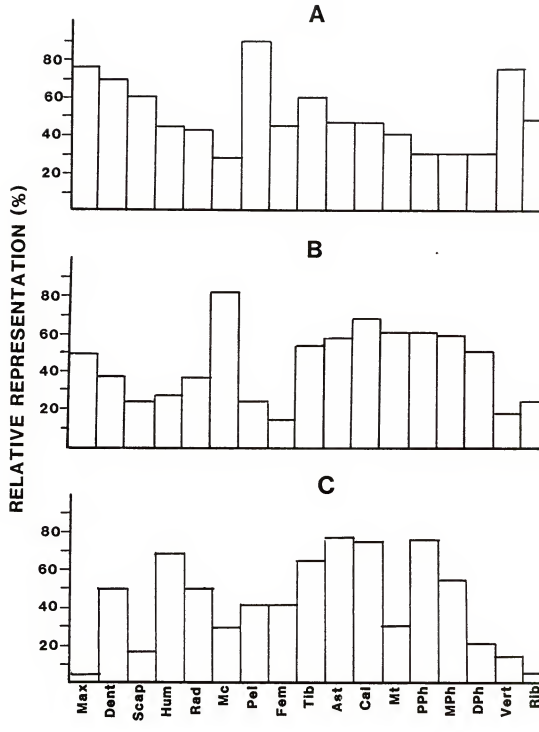

A
B
C
RELATIVE REPRESENTATION (%)
80
60
40
20
Max
Dent
Scap
Hum
Rad
Mc
Pel
Fem
Tib
Ast
Cal
Mt
PPh
MPh
DPh
Vert
Rib

Figure 4-16. Relative representations of skeletal elements in modern and fossil assemblages. a) Artiodactyl remains from a kill site (Binford, 1981) b) Artiodactyl remains from a carnivore den site (Binford, 1981); c) Parahippus remains from unit 11. For list of abbreviations see Figure 4-14.

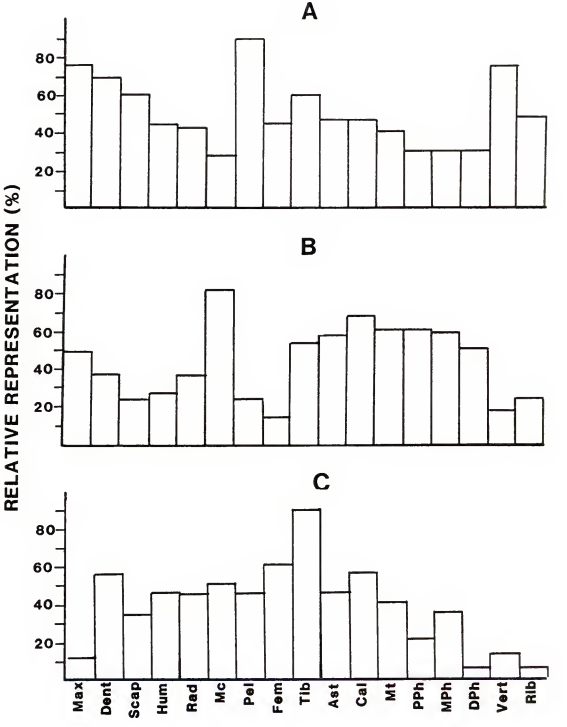

A
B
C
RELATIVE REPRESENTATION (%)
80
60
40
20
Max
Dent
Scap
Hum
Rad
Mc
Pel
Fem
Tib
Ast
Cal
Mt
PPh
MPh
DPh
Vert
Rib

Table 4-1. Relative abundances of genera of megafaunal taxa from the Thomas Farm locality. A) Unit 5; B) Unit 6; C) Unit 7; D) Unit 8; E) Unit 11; F) Unit 15.

A. UNIT 5 Taxon	number of specimens	percent of total	MNI	percent of total
Chelonia (total)	27	6.3	5	19.3
Geochelone	12	2.8	2	7.7
Pseudemys	9	2.1	3	11.6
Crocodylia				
Alligator	180	41.7	3	11.6
Carnivora(total)	28	6.5	6	23.1
Amphicyon	2	0.5	1	3.8
Cynodesmus or Tomarctus	15	3.5	2	7.7
small canid	1	0.2	1	3.8
small mustelid	9	2.1	1	3.8
Hemicyon	2	0.5	1	3.8
Artiodactyla(total)	30	6.9	6	23.1
Nothokemas or Floridatragulus	5	1.2	2	7.7
Prosynthetoceras	2	0.5	1	3.8
Blastomeryx	14	3.3	2	7.7
Machaeromeryx	7	1.6	1	3.8
Perissodactyla(tot.)	166	38.5	7	26.9
Parahippus	108	25.1	3	11.4
Archaeohippus	57	13.2	2	7.7
Anchitherium	2	0.5	1	3.8
Floridaceras	1	0.2	1	3.8
TOTAL	431	100.0	26	100.0
B. UNIT 6				
Chelonia (total)	49	6.3	4	9.3
Geochelone	28	3.6	2	4.7
Pseudemys	12	1.5	2	4.7
Crocodylia				
Alligator	207	26.4	3	6.9
Carnivora(total)	58	7.4	10	23.3
Amphicyon	7	0.9	2	4.7
Cynelos	1	0.1	1	2.3
Cynodesmus or Tomarctus	33	4.2	2	4.7
small canid	2	0.3	1	2.3
Leptarctus	4	0.5	2	4.7
small mustelid	5	0.6	1	2.3
Hemicyon	1	0.1	1	2.3

Table 4-1--continued.

Taxon	number of specimens	percent of total	MNI	percent of total
Artiodactyla(total)	83	10.6	9	20.9
Nothokemas or Floridatragulus	9	1.1	2	4.7
Prosynthetoceras	14	1.8	1	2.3
Blastomeryx	38	4.9	3	6.9
Machaeromeryx	21	2.7	2	4.7
Merycoidodon	1	0.1	1	2.3
Perissodactyla(tot.)	387	49.4	17	39.5
Parahippus	253	32.3	9	20.9
Archaeohippus	130	16.6	7	16.3
Floridaceras	4	0.5	1	2.3
TOTAL	784	100.0	43	100.0
C. UNIT 7				
Chelonia (total)	46	6.4	4	12.1
Geochelone	20	2.8	2	6.1
Pseudemys	12	1.7	2	6.1
Crocodylia				
Alligator	136	18.9	3	9.1
Carnivora(total)	42	5.8	6	18.1
Amphicyon	5	0.7	1	3.0
Cynodesmus or Tomarctus	22	3.1	2	6.1
Leptarctus	2	0.3	1	3.0
small mustelid	5	0.7	1	3.0
Hemicyon	1	0.1	1	3.0
Artiodactyla(total)	62	8.6	8	24.3
Nothokemas or Floridatragulus	11	1.5	1	3.0
Prosynthetoceras	20	2.8	3	9.1
Blastomeryx	22	3.1	2	6.1
Machaeromeryx	9	1.3	1	3.0
Desmathyus(?)	1	0.1	1	3.0
Perissodactyla(tot.)	435	60.3	12	36.4
Parahippus	288	39.9	5	15.2
Archaeohippus	144	19.9	4	12.1
Anchitherium	1	0.1	1	3.0
Floridaceras	1	0.1	1	3.0
Diceratherium	1	0.1	1	3.0
TOTAL	721	100.0	33	100.0

Table 4-1--continued.

D. UNIT 8 Taxon	number of specimens	percent of total	MNI	percent of total
Chelonia (total)	34	6.0	3	8.8
Geochelone	17	3.0	2	5.8
Pseudemys	10	1.8	1	2.9
Crocodylia				
Alligator	45	7.9	2	5.8
Carnivora (total)	45	7.9	8	23.5
Amphicyon	3	0.5	1	2.9
Cynelos(?)	4	0.7	1	2.9
Cynodesmus or Tomarctus	28	5.0	3	8.8
small canid	2	0.4	1	2.9
Leptarctus	2	0.4	1	2.9
small mustelid	4	0.7	1	2.9
Artiodactyla(total)	86	15.2	9	26.5
Nothokemas or Floridatraqulus	35	6.2	3	8.8
Prosynthetoceras	14	2.5	2	5.8
Blastomeryx	10	1.8	1	2.9
Machaeromeryx	18	3.2	2	5.8
Merycoidodon	2	0.4	1	2.9
Perissodactyla(tot.)	356	62.9	12	35.3
Parahippus	273	48.3	7	20.6
Archaeohippus	80	14.1	3	8.8
Anchitherium	2	0.4	1	2.9
Floridaceras	1	0.2	1	2.9
TOTAL	566	100.0	34	100.0
E. UNIT 11				
Chelonia (total)	18	2.7	2	5.4
Geochelone	17	2.7	2	5.4
Crocodylia				
Alligator	13	1.9	2	5.4
Carnivora(total)	67	10.2	9	24.3
Amphicyon	7	1.1	1	2.7
Cynelos(?)	2	0.3	1	2.7
Cynodesmus or Tomarctus	20	3.0	3	8.1
small canid	1	0.2	1	2.7
Leptarctus	2	0.3	1	2.7
small mustelid	7	1.1	1	2.7
Hemicyon	4	0.6	1	2.7

Table 4-1--continued

Taxon	number of specimens	percent of total	MNI	percent of total
Artiodactyla(total)	79	12.0	9	24.3
Nothokemas or Floridatragulus	42	6.4	2	5.4
large camelid	1	0.2	1	2.7
Prosynthetoceras	11	1.7	2	5.4
Blastomeryx	8	1.2	1	2.7
Machaeromeryx	12	1.8	1	2.7
Desmathyus	2	0.3	1	2.7
Perissodactyla(tot)	481	73.1	15	40.5
Parahippus	350	53.2	9	24.3
Archaeohippus	108	16.4	4	10.8
Anchitherium	2	0.3	1	2.7
Floridaceras	2	0.3	1	2.7
TOTAL	658	100.0	37	100.0
F. UNIT 15				
Chelonia (total)	3	1.8	2	11.1
Geochelone	2	1.2	1	5.6
Pseudemys	1	0.6	1	5.6
Crocodylia				
Alligator	31	18.6	1	5.6
Carnivora (total)	28	16.9	7	31.8
Cynodesmus or Tomarctus	16	9.6	1	5.6
small canid	3	1.8	2	11.1
Leptarctus	5	3.0	1	5.6
Miomustela(?)	23	13.8	2	11.1
small mustelid	4	2.4	1	5.6
Artiodactyla(total)	41	24.7	5	27.7
Prosynthetoceras	7	4.2	1	5.6
Blastomeryx	5	3.0	1	5.6
Machaeromeryx	29	17.5	3	16.7
Perissodactyla(tot.)	63	37.9	3	16.7
Parahippus	28	16.9	1	5.6
Archaeohippus	35	21.1	2	11.1
TOTAL	166	100.0	17	100.0

Table 4-2. Relative representations of elements of Parahippus leonensis from major sedimentary units at the Thomas Farm locality.

UNIT 5 MNI=3 Element	Number	Relative Representation	UNIT 6 MNI=9 Number	Relative Representation
Maxilla	0	0	0	0
Petrosal	3	50.0	2	11.1
Dentary	3	50.0	5	27.7
Incisor	8	22.2	7	6.5
Cheektooth	13	19.0	11	10.3
Scapula	1	16.6	4	22.2
Humerus	1	16.6	7	38.9
Radius	4	66.6	4	22.2
Ulna	2	33.3	4	22.2
Scaphoid	2	33.3	4	22.2
Cuneiform	2	33.3	2	11.1
Pisiform	1	16.6	4	22.2
Magnum	1	16.6	5	27.8
Lunar	0	0	0	0
Unciform	1	16.6	6	33.3
Trapezium	0	0	1	5.6
Metacarpal II	2	33.3	5	27.8
Metacarpal III	4	66.6	1	5.6
Metacarpal IV	2	33.3	3	16.6
Innominate	3	50.0	4	22.2
Femur	2	33.3	5	27.8
Patella	1	16.6	5	27.8
Tibia	2	33.3	11	61.1
Calcaneum	0	0	12	66.7
Astragalus	1	16.6	6	66.6
Navicular	2	33.3	7	38.9
Cuboid	1	16.6	3	16.7
Entocuneiform	2	33.3	0	0
Mesoentocun.	0	0	1	5.6
Ectocuneiform	2	33.3	1	5.6
Metatarsal II	2	33.3	2	11.1
Metatarsal III	0	0	3	16.7
Metatarsal IV	4	66.6	5	27.7
Lat. Metatarsal	9	37.5	10	11.1
Pr.Phalanx III	4	33.3	16	44.4
Med. Phalanx III	4	33.3	15	41.7
D.Phalanx III	0	0	3	8.3
Pr. Lat. Phalanx	12	50.0	11	15.3
M. Lat. Phalanx	5	20.8	6	8.3
D. Lat. Phalanx	4	16.6	3	4.2
Rib	4	3.7	8	2.5
Vertebra	9	9.6	30	9.3

Table 4-2--continued.

Element	UNIT 7 MNI= 5 Number	Relative Representation	UNIT 8 MNI= 7 Number	Relative Representation
Maxilla	0	0	1	14.3
Petrosal	4	40.0	3	21.4
Dentary	4	40.0	9	64.3
Incisor	13	21.6	7	9.5
Cheektooth	46	36.5	19	9.7
Scapula	2	20.0	0	0
Humerus	4	40.0	11	78.5
Radius	5	50.0	10	71.4
Ulna	5	50.0	8	57.1
Scaphoid	9	90.0	10	71.4
Cuneiform	3	30.0	2	14.3
Pisiform	4	40.0	1	7.1
Magnum	7	70.0	2	14.3
Lunar	3	30.0	3	21.4
Unciform	7	70.0	2	14.3
Trapezium	1	10.0	2	14.3
Metacarpal II	4	40.0	3	21.4
Metacarpal III	7	70.0	2	14.3
Metacarpal IV	1	10.0	2	14.3
Innominate	4	40.0	4	28.6
Femur	5	50.0	5	35.7
Patella	1	10.0	6	42.8
Tibia	7	70.0	8	57.1
Calcaneum	6	60.0	9	64.3
Astragalus	5	50.0	14	100.0
Navicular	4	40.0	10	71.4
Cuboid	9	90.0	5	35.7
Entocuneiform	0	0	0	0
Mesoentocun.	5	50.0	0	0
Ectocuneiform	1	10.0	3	21.4
Metatarsal II	4	40.0	5	35.7
Metatarsal III	5	50.0	2	14.2
Metatarsal IV	6	60.0	4	28.6
Lat. Metatarsal	18	33.3	12	21.4
Pr. Phalanx III	13	65.0	22	78.6
Med. Phalanx III	15	75.0	8	28.6
D. Phalanx III	6	30.0	4	14.3
Pr. Lat. Phalanx	19	47.5	15	26.8
M. Lat. Phalanx	12	30.0	4	11.1
D. Lat. Phalanx	1	5.0	3	10.7
Rib	7	3.8	11	4.4
Vertebra	22	12.2	35	13.8

Table 4-2--continued

Element	UNIT 11 MNI= 9 Number	Relative Representation	UNIT 15 MNI= 1 Number	Relative Representation
Maxilla	1(skull)	11.1	0	0
Petrosal	7	38.9	0	0
Dentary	10	55.6	1	50.0
Incisor	20	21.3	4	33.3
Cheektooth	44	17.5	0	0
Scapula	6	33.3	0	0
Humerus	8	44.4	1	50.0
Radius	7	39.0	0	0
Ulna	8	44.4	0	0
Scaphoid	3	16.7	0	0
Cuneiform	0	0	1	50.0
Pisiform	3	16.7	1	50.0
Magnum	4	22.2	0	0
Lunar	3	16.7	0	0
Unciform	0	0	0	0
Trapezium	0	0	0	0
Metacarpal II	2	11.1	0	0
Metacarpal III	9	50.0	0	0
Metacarpal IV	1	5.6	0	0
Innominate	8	44.4	1	50.0
Femur	11	61.1	1	50.0
Patella	4	22.2	0	0
Tibia	16	88.9	0	0
Calcaneum	10	55.6	0	0
Astragalus	8	44.4	0	0
Navicular	6	33.3	1	50.0
Cuboid	4	22.2	0	0
Mesoentocun.	0	0	0	0
Ectocuneiform	8	44.4	0	0
Metatarsal II	7	38.8	1	50.0
Metatarsal III	7	38.8	0	0
Metatarsal IV	13	72.2	0	0
Lat. Metatarsal	13	16.6	0	0
Pr. Phalanx III	7	19.4	1	25.0
Med. Phalanx III	12	33.3	0	0
D. Phalanx III	2	4.2	1	50.0
Pr. Lat. Phalanx	18	25.0	3	37.5
M. Lat. Phalanx	4	6.9	0	0
D. Lat. Phalanx	1	1.8	4	50.0
Rib	15	4.6		
Vertebra	37	11.4		

Table 4-3. Relative representations of elements of Parahippus leonensis from combined units 6, 7, and 8.

MNI=17

Element	Number	Relative Representation
Maxilla	1	2.9
Petrosal	9	26.5
Dentary	17	50.0
Incisor	26	12.9
Cheektooth	80	16.8
Scapula	6	17.6
Humerus	23	67.6
Radius	17	50.0
Ulna	14	41.2
Scaphoid	23	67.6
Cuneiform	7	20.5
Pisiform	5	14.7
Magnum	14	41.2
Lunar	15	44.1
Unciform	15	44.1
Trapezium	4	11.7
Metacarpal II	11	32.3
Metacarpal III	10	29.4
Metacarpal IV	6	17.6
Innominate	14	41.2
Femur	14	41.2
Patella	12	35.3
Tibia	22	64.7
Calcaneum	27	76.4
Astragalus	25	73.5
Navicular	21	61.6
Cuboid	17	50.0
Mesoentocun.	6	17.6
Ectocuneiform	5	14.7
Metatarsal II	11	32.3
Metatarsal III	10	29.4
Metatarsal IV	15	44.1
Lat. Metatarsal	40	29.4
Pr. Phalanx III	51	75.0
Med. Phalanx III	38	55.5
D. Phalanx III	13	19.2
Pr. Lat. Phalanx	45	32.3
M. Lat. Phalanx	18	13.2
D. Lat. Phalanx	6	4.4
Rib	26	4.2
Vertebra	87	14.2

Table 4-4. Voorhies dispersal groups of *Parahippus leonensis* elements from unit 5. Abbreviations: d., distal; med., medial; pr., proximal; rel. rep., relative representation. Upper case lettering indicates elements with greater than 50% representation.

I	I/II	II	II/III	III	Rel. Rep.
	PR. LAT PHALANX	RADIUS METAPODIAL PELVIS	DENTARY PETROSAL		>50
cuneiform	ectocuneiform ulna scaphoid	femur tibia			>40
	pr. phalanx III med. phalanx III navicular				>30
incisor m. lat. phalanx					>20
cheektooth pisiform	scapula magnum	humerus astragalus			
d. lat. phalanx	unciform patella cuboid				>10
trapezium mesoentocun.	lunar	calcaneum		maxilla	
d. phalanx III vertebra rib					> 0

Table 4-5. Voorhies dispersal groups of Parahippus leonensis elements from combined unit 6-8. For list of abbreviations see Table 4-4.

I	I/II	II	II/III	III	Rel. Rep.
NAVICULAR	RADIUS	DENTARY			
	SCAPHOID	HUMERUS			>50
	CUBOID	ASTRAGALUS			
	PR. PHALANX III	CALCANEUM			
	MED. PHALANX III	TIBIA			
	ulna	femur			
	lunar	pelvis			
	magnum				
	unciform				>40
pr. lat phalanx	patella	metapodial			
cuneiform					>30
trapezium	scapula		petrosal		>20
cheektooth	ectocuneiform				
mesoentocun.					
incisor					
med. lat phalanx					>10
pisiform					
vertebra					
d. phalanx III					
d. lat. phalanx				maxilla	>0

Table 4-6. Equivalent quartz grain diameters (dq_n) for selected elements of *Parahippus leonensis*. Calculations described in text.

Element	dq_n (mm)	
	Dry	Wet
Humerus (distal)		13.96
Ulna (proximal)		3.1
Tibia (distal)		16.02
Scaphoid	1.16	3.14
Lunar	1.38	2.69
Magnum	1.13	1.56
Unciform	2.41	2.41
Calcaneum	1.81	5.62
Astragalus	1.18	3.42
Navicular	2.34	3.12
Cuboid	0.09	2.15
Prox. Phalanx III	0.24	1.59
Med. Phalanx III	0.22	0.44

Table 4-7. Voorhies dispersal groups of Parahippus leonensis elements from unit 11. For list of abbreviations see Table 4-4.

I	I/II	II	II/III	III	Rel. Rep.
		FEMUR	DENTARY		
		METAPODIAL			>50
		TIBIA			
		CALCANEUM			
	ulna	humerus			
	ectocuneiform	pelvis			>40
		astragalus			
	scapula	radius	petrosal		
	navicular				>30
	med. phalanx III				
incisor	magnum				
pr. lat. phalanx	patella				>20
	cuboid				
cheektooth	scaphoid				
pisiform	lunar			maxilla	
vertebra	pr. phalanx III				>10
cuneiform	unciform				
trapezium					
entocuneiform					
mesoentocuneiform					
med. lat phalanx					> 0
d. phalanx III					
d. lat. phalanx					
ribs					

Table 4-8. Voorhies dispersal groups of artiodactyl elements from a wolf kill site.+ For list of abbreviations, see Table 4-4.

I	I/II	II	II/III	III	Rel.
VERTEBRA	SCAPULA	PELVIS	DENTARY	SKULL	Rep.
		TIBIA			
ribs	carpals	femur			>50
		humerus			
		radius			>40
		astragalus			
		calcaneum			
dist. phalanx	prox. phalanx	metapodial			
	med. phalanx				>30

+ data from Binford, 1981

Table 4-9. Voorhies dispersal groups of equid elements from unit 15. For list of abbreviations see Table 4-4.

I	I/II	II	II/III	III	Rel. Rep.
					>50
cuneiform	ectocuneiform	patella	ulna	maxilla	>40
pisiform					>30
incisor			tibia(epiph)		
lat. phalanges					>20
mesoentocuneiform					
cheektooth	phalanges III		jaw condyle		>10
metapodial			humerus		
			limb bones(0)		> 0

CHAPTER 5
MICROFAUNAL TAPHONOMY

An assemblage of small vertebrates can provide information on the type of depositional environment and taphonomic factors responsible for the formation of the accumulation. While many aspects of microfauna to be examined are similar to those studied for megafauna, analysis of microfaunal deposits is treated in a somewhat different manner than that of megafaunal assemblages.

Sample Size

Sample size of a microfaunal assemblage is a function of the amount of sediment, by dry weight, that is processed to obtain microvertebrate taxa. The volume of matrix that must be washed in order to recover a sample of microfauna is dependent on the richness of the matrix, and varies from site to site. Although over 1,200 kg of matrix was washed and sorted in this study, the total dry weight of sediment taken from each major layer did not exceed 220 kg. Ideally, the greater the volume processed, the better the microvertebrate sample; however, time constraints prevented further collection and processing of a larger volume of sediment. The microvertebrate samples used in this analysis (and in Chapter 11) were obtained from washing approximately 200 kg of matrix from each of the four major bone-bearing levels. The levels analyzed and matrix weights are listed in Table 5-1. Units 6 and 7 are similar lithologically and faunally and were lumped in order to provide a sample of sufficient weight for comparision with other layers. Microfauna from Unit 8 was

omitted from the study, as not enough matrix was collected from this layer to allow its inclusion.

It is difficult to determine if a given amount of sediment adequately samples the microfauna present. A general assessment may be made by plotting the cumulative number of taxa obtained in succeeding samples taken from a particular layer or locality. When the curve approaches the asymptote, it is inferred that the majority of species represented have been collected (Wolff, 1975). Comparison of cumulative curves for different collecting sites within a locality indicates if sample sizes are adequate, and also provides evidence of similarities or differences in faunal content between the samples.

Figure 5-1 shows the curves of cumulative microvertebrate species obtained in the course of matrix collection. In units 5, 6-7, and 11, the number of microvertebrate taxa reaches its upper limit at about 34 species. The total number of microvertebrate species known from the Thomas Farm, including several undescribed taxa, is 51. Species recovery was therefore 66% in the 200 kg matrix samples of these units. The curve for unit 15 does not show a clear plateau, indicating that 200 kg of matrix does not adequately sample the microvertebrate taxa in this layer. However, the representation of microfaunal taxa is 78%. Several of the taxa found in unit 15 are those which are considered very rare, and the overall numbers specimens recovered are far greater than those of any other unit. Processing an additional 200 kg of matrix from this layer resulted in the addition of only 2 more species to the number collected in the first sample (40 to 42). Based on the above observations, I conclude that the amount of sediment processed from unit 15 is sufficient to

provide a reliable sample of the microfauna present. The similarity of the shape of the curves for the lower sedimentary layers not only indicates that microfauna sample sizes are large enough to permit comparisons between layers, but also shows that in terms of microfauna, the lower layers are of similar richness, while unit 15 is considerably more productive.

Most microvertebrate taphonomy studies to date have dealt only with small mammals rather than with non-mammalian groups. Two basic models have been presented to account for potential sources of most micromammal accumulations; coprocoenoses and fluvial deposits.

Mellett (1974) proposed that some microvertebrate fossil assemblages are the remains of large accumulations of predator scat. He illustrated that coprocoenoses, as he termed them, can be recognized by characteristic bone breakage patterns caused by the carnivore involved, and that skeletal remains are often partially destroyed by passage through the predator's digestive system.

Mayhew (1977) demonstrated that small mammal bones from hawk pellets show characteristic features of breakage and corrosion by stomach acid. Korth (1979), Pratt (1979), and Dodson and Wexlar (1979) investigated the condition of mammalian bones found in owl pellets and determined relative representations of mammalian elements from owl pellet accumulations. Korth (1979) also extracted skeletal remains from coyote scat and compared the relative representations of bones from recent scat to preservaton of microvertebrate fossils in several assemblages from Nebraska. Fisher (1981a, b, c) demonstrated that bone digested by alligators is altered characteristically, and attributed an accumulation of small Paleocene mammals to this type of

coprocoenosis. Andrews and Nesbit Evans (1983) analyzed scat of a number of modern mammalian carnivores, and determined relative representation of the elements found in each type of feces. Maas (1985) summarized the diagnostic features of bone accumulations formed by various types of carnivores.

A microvertebrate assemblage may alternatively be formed by fluvial deposition. The agent of accumulation is water flow of a particular velocity which concentrates elements with similar hydrodynamic properties. Although studies have been conducted that demonstrate the fluvial behavior of larger vertebrate bones (Voorhies, 1969; Behrensmeyer, 1975), few investigations have dealt with the fluvial behavior of bones of small vertebrates. Dodson (1973) illustrated that frog and mouse elements are highly susceptible to transport by running water, although if current velocities are not sufficient to transport all small elements, dispersal groups may be formed. Wolff (1973) showed that relative representations of microvertebrate elements from the Pleistocene Rodeo locality had been affected by fluvial factors. Korth (1979) calculated quartz grain equivalents for micromammal skeletal elements and showed that at a fluvially deposited site, the most abundant microvertebrate elements are similar in equivalent quartz grain size to the mean grain size of the associated sediment.

The similarities of the microvertebrate accumulations from the Thomas Farm locality to each of these two basic models will be investigated. Before this step can be undertaken, it is first necessary to examine the characteristics of each type of deposit, such as physical condition of bones, faunal composition, and relative

representations of skeletal elements. Bone orientation will not be considered, as microvertebrate remains are too small to provide field data necessary for this type of analysis.

Coprocoenoses

Coprocoenoses possess a number of distinctive characteristics that allow for the recognition of a predator-accumulated fossil assemblage. Some of these features are general and apply to a a wide range of predators, while others may be specific enough to allow identification of the type of predator (e.g. mammalian, avian, reptilian) responsible for a particular assemblage. The diagnostic features of a coprocoenosis are;

1. Physcial features on bone, including characteristic breakage and fracture patterns resulting from the predator's method of feeding (Mellett, 1974), and the effects of acid on tooth enamel and bone (Mayhew, 1977; Fisher, 1981a, b, c). Many of these features, while not evident to the naked eye, can be discerned by microscopic or SEM analysis (Rensberger, pers. comm.).
2. Faunal composition. The relative abundances of the species found in the deposit, or the predominance of vertebrates of a certain size range may indicate if a microvertebrate accumulation was formed by a carnivore. Various mammalian and avian predators are known to exhibit preferences for certain prey types, or a specific size range of prey (Rosenzweig, 1966, 1968; Ewer, 1973).
3. Bone relative representations and preservation biases. Elements may be selectively discarded or destroyed by carnivores, and will therefore be underrepresented in a coprocoenosis. Preferential preservation of one portion of a bone may also be

characteristic of damage caused by a particular type of carnivore.

Recognition of the features listed above would clearly establish carnivore scat as the source of deposit, but there are several cautionary points that must be considered. Comparative studies on recent carnivore scat are not numerous enough to show the range of variation in scatological deposits formed by a specific predator. Table 5-2 illustrates this point. Relative representations of elements of small mammals from coyote scat obtained in two different studies (Korth, 1979; Andrews and Nesbitt-Evans, 1983) are listed. The variation between the two studies is due to a number of factors including the body size and specific feeding behavior of each coyote involved, the types of prey items, and the possible bias against recovery of small elements in scat analysis. Variation is greatest for mammalian predators that chew their prey. Representation of skeletal elements in owl pellets, particularly those cast by owls that swallow prey whole, appears to be more predictable (Morgan, 1977; Korth, 1979; Dodson and Wexlar, 1979; Pratt, 1979).

The most obvious problem associated with using Recent scatalogical studies to document carnivore effects on bone is the selection of a modern carnivore whose feeding behavior can be compared with that of a fossil predator. It is necessary not only to compare aspects of the Recent and fossil bone assemblages, but also to be familiar with the general body size and morphology of a fossil carnivore in order to select a recent comparative analog. Another problem encountered in the interpretation of fossil accumulations is that unless the bone is actually enclosed in fossilized scat, it is nearly impossible to state that a single species of carnivore was responsible for the formation

of a given microvertebrate deposit. This problem is of great interest at a locality such as the Thomas Farm from which a diverse fauna of mammalian and avian predators is known.

Fluvial Deposition

Evidence for fluvial deposition of microvertebrate accumulations is usually based on geologic factors. Most studies on microvertebrate bone transport have been performed on localities where fluvial effects are undoubtedly of overwhelming significance (Wolff, 1973; Korth, 1979). At the Thomas Farm locality, there is no clear indication of a fluvial environment in the classic sense; however, the possibility that the assemblage reflects transport caused by moving water will be investigated. The characteristics considered important in determining the presence of fluvially sorted microfauna are the same as those examined in the determination of a coprocoenosis and are, as follows;

1. Physical destruction such as that caused by water wear. Although this type of damage may be readily identified on large bones, it is usually hard to discern on microvertebrate elements. Korth (1979) and Pratt (1979) performed experimental abrasion studies on small mammal remains, and showed that bones of microvertebrates are modified by water and sand wear. In highly energetic fluvial systems, only the most durable portions of small bones may survive.

2. Faunal composition. Little is known concerning the expected taxonomic diversity of microfauna in a fluvial deposit. The presence of a species in a stream deposit is a function of chance rather than its being the preferred, or non-preferred prey item of a particular predator. Unless a fluvially-laid accumulation

is initially derived from a coprocoenosis, its species diversity and equitability should therefore be greater than that of a coprocoenosis. It is also likely that, in addition to terrestrial vertebrates, those species normally found in fluvial or aquatic environments (fish) would be well represented in a fluvial fossil deposit.

3. Relative representation of elements. Preservation ratios of skeletal elements provide the best evidence that an assemblage has been sorted by running water. A specific current speed would be indicated by an accumulation of elements possessing similar hydrodynamic properties. As was shown for megafaunal remains, there is no one ideal relative representation histogram that indicates fluvial deposition. The types and number of bones represented are dependent on the current speed, and the distance of element transport. Abundance patterns of bones in fluvial environments can be grouped into the four types described by Hanson (1980:491).

In order to identify dispersal groups of small bones, it is necessary to assess the hydraulic behavior of these elements, either by determination of quartz grain equivalents (as was accomplished for megafaunal elements), or by observation of the bones in running water. The former method was used by Korth, who derived predictive equivalences based on an element's settling velocity and the size of the foramen magnum of the animals skull. Dodson (1973) presented a sequence of transport of microvertebrate bones based on their behavior in a flume.

The three features discussed above will be considered in the study of the Thomas Farm microfauna. The assemblage of microcvertebrates from

each layer will be examined, beginning with the upper Unit 15 which contains by far the largest quantity of microfauna of all the layers. The discussion will deal primarily with the most highly represented taxa, the rodents and anurans.

1. Physical Features

Microvertebrate Bones From Unit 15

Evidence of fluvial abrasion is often hard to discern on small bones, particularly those prone to breakage. Elements of the small heteromyid Proheteromys floridanus recovered from unit 15 matrix showed evidence of breakage and acid destruction caused by predators. Most bones showed no evidence of water wear.

The condition of rodent incisors provides convincing evidence that an accumulation represents a coprocoenosis formed by a carnivore. Hydrochloric acid dissolves the outer enamel and dentine layers on the chisel-shaped occlusal surface of the incisor, giving the end of the tooth a whittled appearance. Incisors abraded by sand and water in a tumbling barrel for 7 days also show wear on the ends of the incisors; however, under a dissecting microscope the surface of the incisor can be seen to be smoothly and uniformly worn, unlike that of the ingested tooth. The effect of acid on rodent incisors was first pointed out by Mayhew (1977), who showed that incisors regurgitated by hawks have undergone this distinctive type of modification. My studies on microvertebrate bone destruction by predators have shown that hawks (red-tailed hawk, sharp-shinned hawk) and mammalian predators (coyote, bobcat, weasel) cause destruction of the incisor. The damage is most extensive on incisors that have been eaten by hawks. Incisors from pellets of great horned owls and barn owls are unmodified.

Many of the rodent cheekteeth from unit 15 have corroded enamel, which is powdery in appearance. The occlusal surface of the tooth, particularly around worn cusps, may be destroyed. Fluvial abrasion can also cause cusp destruction of cheekteeth, but the enamel of these teeth appears shiny and the roots are often broken off or worn away. Acid-etched teeth usually possess complete roots, and that part of the tooth that was protected below the gum line is not modified. Teeth that have fallen out of the jaw or skull during digestion also possess roots, but the roots often have a whittled shape.

Many of the postcranial elements of Proheteromys floridanus in unit 15 in possess sharp fractures characteristic of pre-depositional breakage (Korth, 1979; Hill, 1980; Shipman, 1981). Some of the broken edges appear to have been smoothed and rounded, but whether this feature was caused by water abrasion or solution by acid is unclear.

Bones of anurans, in particular bufonids, are numerous in unit 15. Many of the elements show signs of destruction indicative of carnivore ingestion. The bones most frequently found broken show similar breakage patterns to those found in barn owl pellets. This similarity does not mean that owls were the agents of accumulation of the toads, but it may indicate that these remains were deposited by some type of an avian predator. Analysis of pellets of raptors known to eat anurans is needed before definite conclusions can be drawn concerning the condition of the frog remains.

The elements of the other species in the unit 15 microvertebrate fauna do not show evidence of ingestion by carnivores, or of fluvial abrasion. Many of the bat specimens are in excellent condition and complete dentaries and limb bones are found. Most breakage of bat

elements occurs in sediment processing and washing. Few of the cheekteeth show evidence of acid corrosion, indicating these animals were either not prey items, or their bones were ingested by a predator that had little effect on bone destruction.

Birds and reptiles are among the least common vertebrate groups in unit 15 (Table 5-3) and the remains of these animals are often too fragmentary to examine for evidence of predator damage; however, some of the bird bones recovered are in extremely fine condition considering their fragility. Bird bones obtained from hawk pellets are usually subject to a large degree of acid destruction.

Microvertebrate Bones From Units 11 Through 5.

Microvertebrate remains from units 11, 6-7, and 5 show very similar types of bone destruction. Some of the rodent elements from unit 11 show evidence of carnivore-induced bone damage, although the majority of bones from this unit do not. In layers 5 and 6-7, very few of the rodent incisors or cheekteeth show evidence of either carnivore destruction or water wear. Limb bones of microvertebrates are rare in these units, and those recovered are very fragmentary.

2. Faunal Composition

The Thomas Farm Microvertebrate Fauna

Table 5-3 lists numbers and relative abundances of microfaunal taxa from Thomas Farm. Faunal diversity within each of the major layers is shown graphically in terms of numbers of specimens per order and MNI per order in Figures 5-2 and 5-3 respectively.

In considering microfaunal abundance and diversity in terms of numbers of identifiable specimens, it is immediately evident that a 200 kg sample of matrix from unit 15 contains much higher numbers of

microvertebrate specimens than do samples from any of the other units. Proportions of specimens per order, especially of rodents and anurans, appear most similar in units 5 and 6-7. These lower units are different from the upper layers 11 and 15, in which approximately 70% of the identifiable specimens belong to rodents. If the data are examined statistically using the R x C test of independence (Sokal and Rohlf, 1981), the proportions of specimens per order in units 5 and 6-7 are significantly different from those in units 11 and 15 at the 0.001 level. Units 5 and 6-7 are also significantly different from one another at the P = 0.001 level. Units 11 and 15 are different at the P = 0.01 but not the P = 0.001 level.

The proportions of MNI per order between the various layers do not appear very different (Figure 5-3). The R x C test of independence (Sokal and Rohlf, 1981) indicates that proportions of individuals per order in unit 15 are significantly different from those of units 5 and 6-7 at the P = 0.001 level, but they are not significantly different from unit those of unit 11. Faunal composition of Unit 11 is not significantly different from any of the lower units at the P = 0.001 level. The results of the comparisons of microvertebrates from the major layers show that values based on numbers of specimens overestimate the differences between layers, while values based on MNIs evidently underestimate differences. The microvertebrate fauna in unit 15 is unlike any of the lower units in both numbers and proportions of specimens and individuals per order. Before a more detailed discussion of similarities and differences of microvertebrate taxa found in various units is pursued, the basic similarity in microfaunal composition of all units should be

addressed, as it provides evidence concerning environment of deposition.

Taxa that are rare in all units are bony fish, marsupials, and insectivores. Fish are represented by small, isolated vertebrae that cannot be identified below the ordinal level (S. Scudder, pers. comm). The low representation of fish at the Thomas Farm contrasts sharply with the numbers found at fluvially deposited sites such as the late Miocene Love site (Webb, MacFadden, and Baskin, 1981) and Haile 19A (G. Morgan, pers. comm.). The fine state of preservation of the few fish remains that have been recovered argues against their having been present at the locality and subsequently destroyed in the fossilization process. The low numbers of fish elements found at the site may indicate that water at the site was from an ephemeral, rather than permanent source, or that the sinkhole was not fed by large, above-ground streams or outlets. The significance of the low representation of marsupials and insectivores is not clear. The marsupial is known from one tooth. Insectivores are often rare in fossil localities, unless they have been accumulated by an avian predator such as an owl.

Microfaunal taxa that are not highly represented at the Thomas Farm include urodeles, squamates, birds, and bats. Table 5-3 shows that several of these taxa are actually represented by large numbers of specimens, but their relative abundances are low compared to the more numerous rodents and frogs. Among the herpetofauna, the urodele fauna consists of 3 species, with the salamandrid Notopthalamus robustus the most common. The aquatic salamander Siren is rare, and the large extinct Batrachosauroides is known from very few specimens.

Based on the life cycle of modern Notopthalamus in Florida, it is presumed that Notopthalamus robustus was entirely aquatic, however, in the northeast United States, members this genus do have a terrestrial eft form (Duellman and Trueb, 1986). The fairly low numbers of aquatic salamanders indicates that permanent water was not a characteristic of the site. The low representation of lizards and snakes in all layers is also notable. Snakes often appear to be underrepresented at fossil localities because large numbers of vertebrae are required to determine minimum numbers of individuals (Grayson, 1978). Lizard remains are extremely delicate and may not survive fossilization, or the lizards may not have been numerous in the areas where fossilization was taking place.

Birds and bats each comprise less than 5% of the total numbers of individuals from any layer. The rarity of these arboreal taxa at fossil localities is usually attributed to their habitat preferences and the delicacy of their bones. It should be kept in mind that even though relatively speaking, these taxa are not common at Thomas Farm, the number of specimens of these groups is high compared to other localities of similar age in Florida (Pratt, in prep.). The presence of bats, particularly in unit 15, indicates the proximity of the fossil deposit to suitable chiropteran living quarters such as caves.

Anurans and rodents are the dominant microfaunal taxa at the Thomas Farm. The majority of rodent specimens represented are those of the tiny heteromyid Proheteromys floridanus. Sciurids are relatively rare, and eomyids are known from only a few isolated cheekteeth. The predominance of one rodent species in the upper

layers 11 and 15 indicates a taphonomic bias towards preservation of the species in these units.

The overall similarities in the types of animals (by order) found throughout the various layers of the site (Table 5-3) indicate a similarity in the habitat sampled throughout the course of deposition. However, a closer look at the species represented in the more abundant orders, in particular the Anura, points to depositional or environmental differences between the layers.

Figure 5-4 shows the abundances of amphibian species, by MNI, found in each major sedimentary unit. Relative abundances of frog species in unit 5 are the least similar to any of the other layers, with a small ranid being the most common amphibian. Bufonids, which dominate the herpetofauna in the other units by more than 2 to 1 over the next most common anuran, are only the third most abundant species in unit 5. Rana specimens are fairly common in unit 6-7, but are rare in units 11 and 15. Acris barbouri is also common in units 5 and 6-7, but is less well-represented in the upper layers. Relative abundances of the treefrog Hyla goini are fairly uniform throughout all layers. The R x C test of independence shows that the proportions of amphibian species in units 5 and 6-7 are not significantly different from one another at the 0.01 level, but are significantly different from those in unit 15. Numbers of anurans in unit 11 are too low to allow statistical comparison. The variation in representation of frog species between the layers can be related to habitat and depositional status of the environment. The small ranid probably preferred aquatic conditions. Although ranids today are known to occur within a wide variety of habitats, those that possess an ilium morphology similar to

that of the Thomas Farm species are strong swimmers and are most frequently found in aquatic environments (Pratt, in prep). Living species of Acris are also commonly found in aquatic habitats, and it is possible that the fossil form may have exhibited such a preference. The predominance of these forms over the more terrestrial toad Bufo in units 5 and 6-7 indicate that standing water must have been present, at least periodically, while these sediments were being deposited. The aquatic salamander Notopthalamus is also most common in unit 5.

Faunal Composition of a Coprocoenosis

The type of bone destruction seen on elements from unit 15 and to a lesser extent, unit 11, indicates that all or part of the microfaunal deposit in these layers is a coprocoenosis. This hypothesis is further supported by the large numbers of microvertebrate specimens (35.53 identifiable specimens per kg) found in the upper unit, compared to about 1/10 that amount found in the lower clay units (4.8 identifiable specimens per kg in unit 5, 3.2 in unit 6-7), and by the high abundance of one type of micromammal (70%), Proheteromys floridanus.

There are too many variables involved to determine, based on relative abundances of microfaunal taxa alone, if an assemblage is a coprocoenosis. It is known that modern mammalian carnivores may select particular types and sizes of prey (Rosenzweig, 1966, 1968; Ewer, 1973), however, variation in prey choice may vary individually, regionally, or seasonally (Berg and Cheness, 1978: Ewer, 1973). Avian predators also show a great deal of variation in the type and numbers of prey consumed. Figures 5-5a (from Trost and Hutchison, 1963) and 5-5b (from Morgan, 1977) show the relative abundances of vertebrates

from barn owl pellets collected in the United States and the West Indies, respectively. The West Indian owls evidently take larger proportions of herpetofauna because appropriately sized rodent prey is not common on these islands.

It is difficult to choose a modern predator for comparison with a presumed fossil predator if the choice is based soley on relative abundances of prey taxa. Difficulties are also encountered in comparing abundances of modern prey groups to those of unrelated fossil groups. In addition, an accumulation of fossil bones is rarely a pure coprocoenosis. An assemblage may be formed by several types of carnivores, both avian and mammalian, or may be a combination of a coprocoensis and an assemblage formed by other means. Unit 15 probably contains microfaunal taxa that were concentrated by a carnivore, and also contains other groups, such as bats and lizards, that were not prey items. The information provided by analysis of relative abundances is not sufficient to resolve this problem.

Faunal Composition of Fluvial Deposits

Faunal composition that is indicative of a fluvial depositional environment is very difficult to identify. Few studies exist that contain reference to abundances of microvertebrates in fluvially-laid sediments. Those studies that have been done deal soley with the micromammalian taxa (Wolff, 1973). Figure 5-6 shows relative abundances (MNI) of micromammals from the fluvial Rodeo locality (Wolff, 1973). A striking feature of this fauna is the high diversity of small mammals, particularly rodents. It is likely that a high diversity of taxa is characteristic of a fluvial deposit that samples a wide range of habitats, as opposed to a sinkhole or trap that

samples primarily those animals found only in the immediate vicinity. It is also possible that the Late Pleistocene micromammal fauna was more diverse than that of the Florida Miocene. Lagomorphs are completely absent from early Miocene sites in Florida, and several Florida localities of this age from Florida are dominated by two species of heteromyid rodent (Wood, 1932; Olsen, 1964a; Pratt, in prep.).

Another characteristic of the Thomas Farm microvertebrate fauna that is different from that of the Rodeo locality is the presence of large numbers of bats, particularly in unit 15. Bats are evidently not common in fluvial sites, even Florida Miocene fluvial deposits that run through karst topography. Only one bat fossil (a distal radius) was reported from the late Miocene Love Site (Webb et al., 1981), although large amounts of matrix were picked for microfauna.

Units 5 and 6-7 are very similar to one another in number of specimens and microfaunal composition (Figures 5-2 and 5-3). Rodents are far less numerous in these lower layers, while frogs are relatively more abundant in these levels than in the upper units 11 and 15. The abundances of micromammals are more similar to those seen in a deposit influenced by running water (Figure 5-6) than to recent mammalian or avian scats and pellets. MNI are low, and several taxa are fairly well-represented in these layers that are absent in the samples from the upper layers. The large unidentified sciurid and a small unidentified eomyid are both found in the lower layers, but not in the upper layers. The large numbers of frogs and the low abundances of birds also do not support the idea that these lower layers were formed by mammalian carnivores.

3. Relative Representation

In this section, skeletal preservation ratios of microfaunal taxa from each layer or groups of layers will be compared with skeletal preservation of microvertebrates in modern raptor pellets and mammal scat, and with relative representations of elements found in fluvial environments. Elements of the two most common taxa Proheteromys floridanus and Bufo praevius are used in the relative representation calculations. These values are listed in Table 5-4 and 5-5.

Relative Representations of Bones From Coprocoenoses

Unit 15. Relative representations of selected elements of Proheteromys floridanus from the unit 15 sample were compared with those of small mammal bone from mammalian scat and raptor pellets (Korth, 1979; Dodson and Wexlar, 1979; Pratt, 1979; Andrews and Nesbit Evans 1983). Relative representations of bones from scat of the mongoose Ichneumia albicauda, the coyote Canis latrans, and the red fox Vulpes vulpes are similar to relative representation values of fossil rodent elements (Figure 5-7). The choice of these particular carnivores for comparison is based in part on their size and morphology (see discussion of carnivores in Chapter 9).

The observed preservation value of a particular element relative to its value in a given scatalogical accumulation provides an observed-to-expected ratio. These calculations are shown in Table 5-6. If the percentage preservation for a particular element in the fossil assemblage is the same as that obtained from a recent scatalogical study, the observed/expected ratio will be 1. An element that is overrepresented in a fossil deposit relative to a scatalogical

deposit will have a preservation ratio greater than 1, while one that is underrepresented will have a value of less than 1.

Comparison of relative representations of Proheteromys floridanus elements from unit 15 with rodent remains from scat of mammalian carnivores shows that 4 elements are higher in abundance in the matrix from unit 15 than they are in scat. The calcaneum, astragalus, and isolated cheekteeth all have higher representation values in the fossil locality than in the three types of scat. The radius is overrepresented in unit 15 relative to mongoose and fox scat but not to coyote scat. Table 5-2 shows that the difference in these values is not necessarily due to extremely high proportions of these elements in the fossil site, but is also related to the fact that several of these bones have low relative representations in scat. It is possible that very small bones may be overlooked in scat analysis (Korth, 1979). Alternatively, their low representation could indicate that these elements were either not eaten, and thus were not defecated at the deposition site, or were ingested and completely destroyed by mechanical or chemical digestion. Podials have low representation values if a predator does not eat the prey's feet; however, the low numbers of radii are harder to explain, especially as the ulna has a fairly high representation in scat. It is likely that the very slender radius is broken in the digestive process, and the small proximal or distal ends are subsequently missed in scat analysis. The low representation of cheekteeth is also difficult to explain. Some carnivores discard the heads of their prey (Andrews and Nesbit Evans, 1983), but this behavior is evidently not characteristic of the carnivores discussed in this study. Maxillae and jaws are highly

represented in these types of scat (Andrews and Nesbit Evans, 1983). If cheekteeth were destroyed by chewing, it is likely that the crania would be destroyed as well. Complete breakdown of cheekteeth by stomach acid is unlikely because teeth apparently are more resistant to complete destruction than are other parts of the skeleton (Fisher, 1981a; Binford, 1981). If low representations of some elements in modern carnivore accumulations are not due to sampling bias, then the higher representations of these elements in the fossil locality may be caused by their concentration by a taphonomic agent such as moving water. This hypothesis will be investigated in the following section.

Fossil elements with relative representation ratios less than 75% of the expected values based on (coyote, fox or mongoose) scat include dentaries and maxilla. This finding seems contradictory, given that cheekteeth and incisors are among the most abundant elements in unit 15. The low preservation ratios of skull and maxillae may be related to their fragility, or may be a function of some sorting process.

Relative representations of fossil elements from unit 15 are not similar to those of bones from modern raptor pellets (Figure 5-8). Large owls, such as the great horned owl and barn owl swallow their prey whole, and most skeletal elements obtained from pellets cast by these animals have higher percentage preservations than P. floridanus elements. The possibility that the microfaunal assemblage from unit 15 represents a raptor accumulation that was sorted by running water will be examined in the following section.

All bones found in red-tailed hawk pellets are partially destroyed by stomach acid (Figure 5-8c). Element types that are

poorly represented or absent are those most severely affected by acid destruction. The lack of similarity between the fossil bone abundances and a bone assemblage formed by a hawk indicates that this type of avian predator was not the sole or primary agent of accumulation the P. floridanus elements.

Little recent comparative data on preservation of anuran elements from scat or pellets is available. Table 5-5 shows relative representation ratios of frog elements compared to their preservation in barn owl pellets from the Cayman Islands (data courtesy of Gary Morgan, 1977). The urostyle and ulna are far more abundant in the fossil accumulation than in recent pellets, but the relative representations of frog elements from unit 15 are not significantly rdifferent from those in the owl pellet accumulation (R x C test of independence, P = 0.01). A more appropriate comparison to the fossil assemblage would be an accumulation formed by a kite; however, no quantitative data on skeletal preservation of prey is available for this bird.

Another important aspect of skeletal element preservation is the portion of the bone (complete, proximal end, distal end) that is represented. Bones that have passed through a predator's digestive tract may show differential survival of one end over another. Table 5-7 lists the relative preservations of ends of selected limb bones of P. floridanus from unit 15. Complete bones are very rare, and most of the long bones consist of a portion of the shaft and one articular end. The preservation ratios of fossil elements are compared with those for bones taken from scat and pellets of mammalian and avian predators. End preservations of 2 of the 3 limb bone types from

mongoose or fox scat are not significantly different from those in the fossil sample (Chi-square goodness of fit test, P =0.01). End preservation proportions of all elements from coyote scat were significantly different from those of the fossil locality. Higher percentages of complete long bones are found in coyote and mongoose scat than are seen in the fossil sample. Bones from raptor pellets show few similarities to the fossil elements with regards to preferred end preservation. Most of the limb bones of small rodents found in great horned owl and barn owl pellets are whole, and those that are not show opposite preferred end preservations to those of the fossil remains (Dodson and Wexlar, 1979). Elements from screech owl and hawk pellets are seldom complete. Bones that have been ingested by hawks usually have one end preserved with much higher frequency over the other end.

The majority of bones of fossil anurans found in unit 15 matrix are incomplete. Of the elements examined in this study, scapulae were the only elements most frequently found whole. Less than 10% of the frog elements collected from the fossil locality are complete. Most humeri are missing the proximal half, the radio-ulna is represented primarily by the proximal end, and the urostyle consists of the posterior articular portion. The lateral processes are usually broken off the sacrum, and the ilium consists of the acetabulum and up to one/third of the iliac shaft. The same elements recovered from barn owl pellets (Morgan, 1977) collected in Cayman Brac were found whole roughly 60% of the time, with the exception of the scapula, of which 94% of the specimens were whole. If the large numbers of anuran elements found in unit 15 were accumulated by a predator, it was

evidently an animal that caused a higher degree of bone breakage than does a barn owl.

Relative Representations of Bones From Fluvial Environments

Unit 15. Potential fluvial action may be determined by testing two hypotheses concerning the bone source. The first assumption is that the original accumulation of microvertebrate bones within unit 15 was caused primarily by small mammalian carnivores, possibly canids, and was later affected by fluvial factors. Therefore the original coprocoenosis had skeletal abundances similar to those of modern scatalogical accumulations. By setting the relative representation values for all elements in scat equal to 100%, the ratio of relative representations of fossil elements to those of the recent accumulation provides a measure of the overrerepresentation or underrepresentation of an element relative to its expected representation in a coprocoenosis. These values are the same as those shown in Table 5-6 and they can now be employed to determine which bones may be highly represented as a result of fluvial sorting. In a fluvial deposit, the most abundant types of elements often share similar hydrodynamic properities. The alternate assumption is that relative representations of fossil bones should not be compared to their expected values in a coprocoenosis because the original source of the bone assemblage was not a scatalogical accumulation, but was formed by other means.

Hydrodynamic similarity of microvertebrate elements (in this case small rodents and anurans) was determined by calculation of equivalent quartz grain diameters based on settling velocities of recent Peromyscus and Rana skeletal elements (Chapter 2, p. 24). These

values are shown in Table 5-8 and are used in the following analysis. The order of relative representations of skeletal elements, based on expected abundances in mammal scat, are shown in Table 5-9. If the fossil micromammals from unit 15 originated from a carnivore assemblage that was later sorted by running water, then the group of elements with high representation ratio values (corrected representation greater than 90%) are expected to be composed of bones with similar quartz grain diameters. Table 5-9 shows the order of representation of elements, from most abundant to least, based on percent preservations corrected for carnivore scat bone preservations. This ranking is compared with that of equivalent grain size rank for each element, from largest equivalent grain size (1) to smallest (13). There is a wide range of variation in size of equivalent quartz grains of the most highly represented elements, indicating that the bones in unit 15 are not a secondarily sorted carnivore deposit. Results are similar if it is assumed that the original accumulation was caused by avian predators (See Table 5-10).

A test of the alternate assumption, that the concentration of microvertebrate remains in unit 15 formed either solely or primarily by moving water, is shown in Table 5-11, which compares the actual relative representation values of rodent elements to their quartz grain equivalent ranks. A large variation in the range of equivalent quartz grain diameter sizes of the most highly represented bones indicates that fluvial transport of the micromammal bones is not strongly supported. Relative representations of anuran elements from unit 15 compared with their respective quartz grain equivalents is shown in Table 5-13. Although the highly represented ilium and ulna

are similar in settling velocity and hence in equivalent quartz grain diameter, the high representation of other elements having both larger and smaller equivalent quartz grain sizes supports the conclusion based on the rodent data that unit 15 was not greatly affected by selective transport.

Examination of the concentration of microvertebrate bones in unit 15 points strongly to the conclusion that this level was the site of a mammalian or avian predator coprocoenosis (or some combination of the two). There is little evidence to suggest that the remains were transported by running water. If it is accepted that the accumulation in unit 15 is a relatively unmodified coprocoenosis, it is now possible to treat the relative representations of elements from this layer as the expected values for a microvertebrate accumulation from Thomas Farm formed by carnivores. The assumptions to be tested for each of the lower sedimentary layers are the same as those examined for unit 15: that the elements represent either an unmodified coprocoenosis, a fluvially sorted coprocoenosis, or a fluvially sorted assemblage that was not initially derived from a scatological deposit.

Unit 11. The mean percentage preservation value of Unit 11 elements is much lower (28%) than that of unit 15 or of a carnivore-formed accumulation, indicating that the bones of this layer do not represent an unmodified coprocoenosis and that other taphonomic factors must have been instrumental in the deposition of this layer. The orders of relative representations of elements in unit 11 based on expected values from unit 15, compared with their equivalent quartz grain diameter rankings (Table 5-11) does not show a clear grouping of elements with similar hydrodynamic properties. Actual relative

representations of elements compared with their quartz grain equivalents indicates that well represented elements (greater than 35% preservation) have similar equivalent grain sizes (Table 5-12). For the most part (with the exception of the tibia, which should be in this group), the elements that are highly represented would be considered lag elements, suggesting the presence of a current sufficient to winnow out some of the lighter, more readily transported elements. The most highly represented anuran elements also have relatively large equivalent quartz grain sizes. I would suggest that the microvertebrate bones in unit 11 were not derived primarily from a coprocoenosis, but were influenced by moving water.

Unit 6-7. Unit 6-7 microfauna has a very low mean percentage preservation value (17.5%), indicating that microvertebrate elements in this layer were probably not deposited by a carnivore, or that if they were, other taphonomic factors have completely obscured the original bone source. The representations of the elements of P. floridanus based on the unit 15 expected values are shown in Table 5-11. The order of the corrected relative representations from highest to lowest are identical to the order of the the actual representations (Table 5-12). The most highly represented elements are very similar to each other in equivalent grain size. The order of element representation is also very similar to that of the Rodeo deposit (Wolff, 1973), a fluvially-laid accumulation. It seems very likely that the microvertebrate remains in unit 6-7, regardless of their original source, were affected by a water current strong enough to cause selective sorting of the elements.

Unit 5. The mean preservation value of elements in unit 5 is slightly higher than that of unit 6-7 (21.5%), but is too low to be indicative of a coprocoenosis. Corrected relative representations based on unit 15 abundances show that all elements have lower than expected representations, but the order of these corrected abundance does not reflect fluvial sorting (Table 5-11). Actual relative representations show the presence of a group of elements that would be transported together in running water. The grouping is not as tight as is seen in the layer 6-7, indicating that the current was weaker or intermittent in unit 5 (Table 5-12).

The similarities of the bone abundances in the lower layers to those of a fluvial model and their lack of similarity to a coprocoenosis indicates that at the time of deposition of these sediments, moving water was present. An estimate of the speed of the current can be determined from the size of the quartz grain equivalents of the most well-represented elements, which in all 3 units are rodent incisors. The representation of this element is high (over 70% in all layers), so it may be assumed that for the most part current speeds were not sufficient to cause its removal. Reference to the predicted current velocity graph (Allen, 1965; Behrensmeyer, 1975) indicates that current speeds of over 35 cm/second would be sufficient to transport this element. Therefore the current in the sink seldom exceeded 30-35 cm/second. This finding agrees well with the proposed current speed based on the megafaunal analysis (Chapter 4).

Figure 5-1. Cumulative numbers of microfaunal species added to fauna with consecutive matrix samples. a) Unit 5; b) Unit 6-7; c) Unit 11; d) Unit 15.

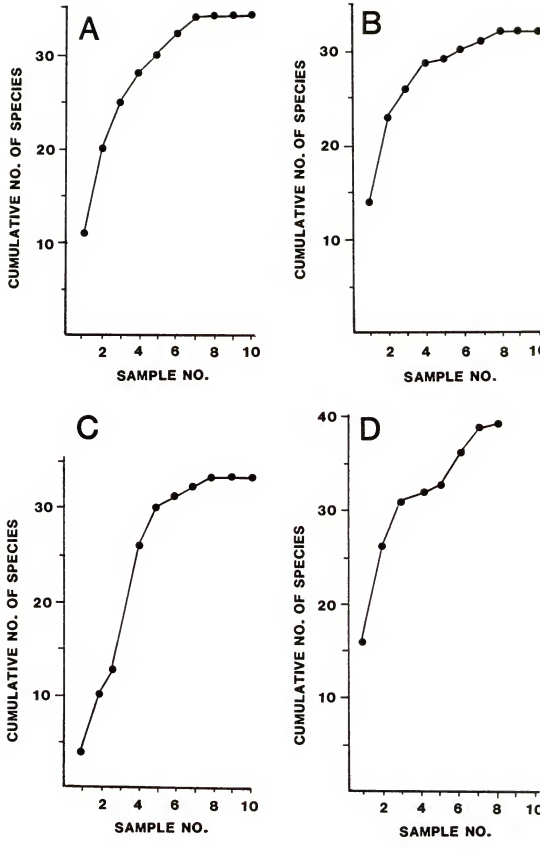

A
B
C
D
CUMULATIVE NO. OF SPECIES
SAMPLE NO.
10
20
30
40
2
4
6
8
10

Figure 5-2. Relative abundances, in numbers of specimens per taxon, of microvertebrates from Thomas Farm. a) Unit 5; b) Unit 6-7; c) Unit 11; d) Unit 15. Abbreviations: AV, Aves; C, Chiroptera; I, Insectivora; O, Osteichthyes; SQ, Squamata; U, Urodela. For numerical values see Table 5-3.

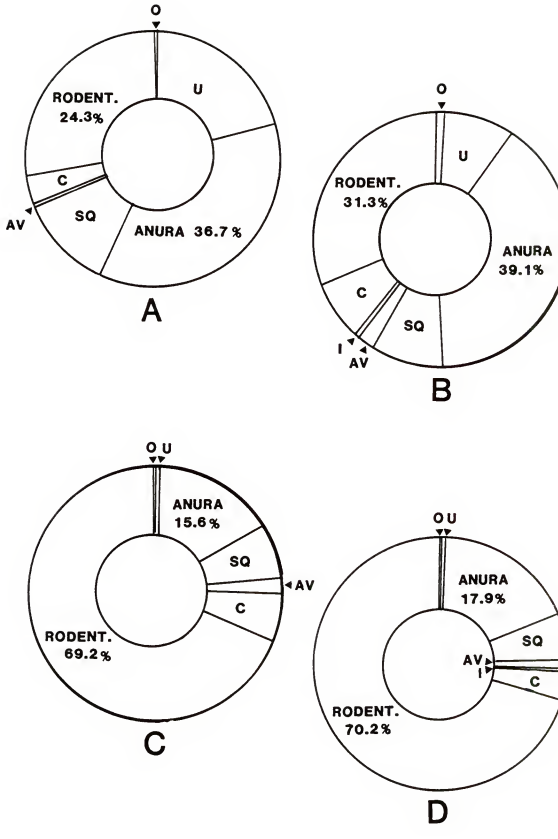
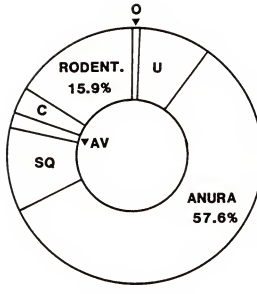
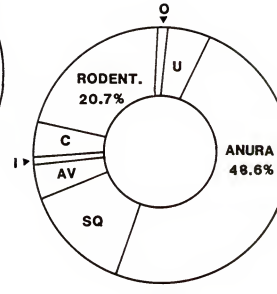

O
U
RODENT.
24.3%
C
AV
SQ
ANURA 36.7%
A
O
U
RODENT.
31.3%
ANURA
39.1%
C
SQ
I
AV
B
O U
ANURA
15.6%
SQ
AV
C
RODENT.
69.2%
C
O U
ANURA
17.9%
SQ
AV
I
C
RODENT.
70.2%
D

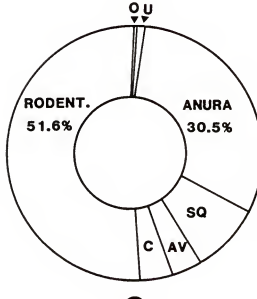
Figure 5-3. Relative abundances, in MNI per taxon, of microvertebrates from Thomas Farm. a) Unit 5; b) Unit 6-7; d) Unit 11; e) Unit 15. See Figure 5-2 for list of abbreviations. For numerical values see Table 5-3.


O
RODENT.
15.9%
U
C
AV
SQ
ANURA
57.6%

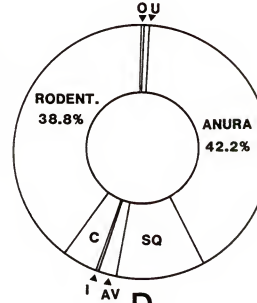
A


O
RODENT.
20.7%
U
C
I
AV
SQ
ANURA
48.6%

B


O U
RODENT.
51.6%
ANURA
30.5%
SQ
C
AV

C


O U
RODENT.
38.8%
ANURA
42.2%
C
SQ
I
AV

D

Figure 5-4. Relative abundances, in MNI per genus, of amphibians from Thomas Farm. a) Unit 5; b) Unit 6-7; d) Unit 11; e) Unit 15. Abbreviations: Ac, Acris; Bu, Bufo; Hy, Hyla; Ra, Rana; No, Notopthalamus; S, Siren; Sc, Scaphiopus.

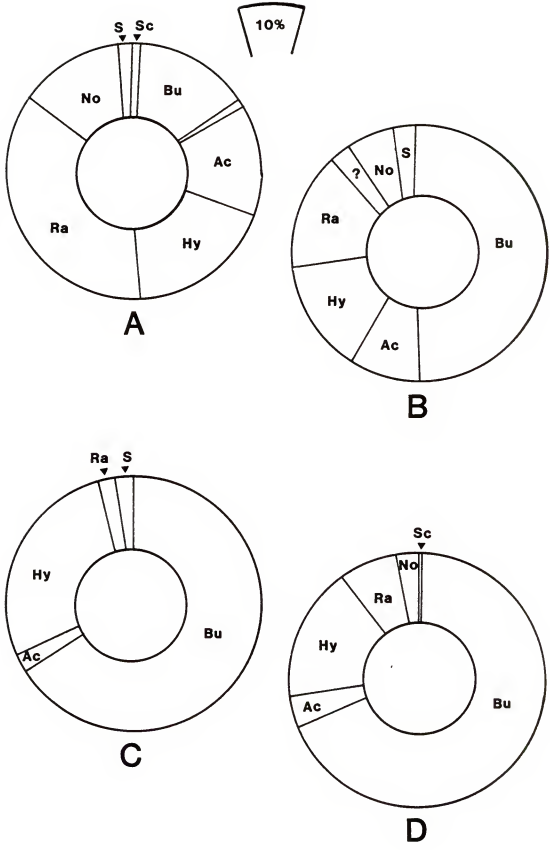

10%
S
Sc
No
Bu
Ac
Ra
Hy
A
S
?
No
Ra
Bu
Hy
Ac
B
Ra
S
Hy
Bu
Ac
C
Sc
No
Ra
Hy
Ac
Bu
D

Figure 5-5. Relative abundances, in MNI per taxon, of microvertebrates from modern barn owl pellets. a) Florida barn owl (data from Trost and Hutchison, 1963); d) Cayman Islands barn owl (data from Morgan, 1977). Abbreviations: AM, Amphibia; AV, Aves; C, Chiroptera; IN, Insectivora; LAG, Lagomorpha; RODENT, Rodentia; SQ, Squamata.

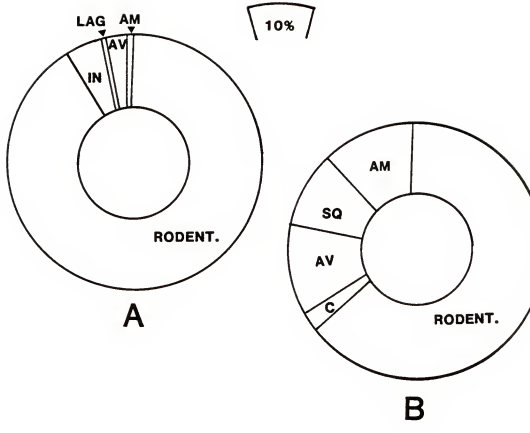

LAG
AM
AV
IN
RODENT.
A
10%
AM
SQ
AV
C
RODENT.
B

Figure 5-6. Relative abundances, in MNI per taxon, of micromammals from (a through e) Thomas Farm, and (f), Rodeo locality (data from Wolff, 1973). a) Unit 5; b) Unit 6-7; c) Unit 11; d) Unit 15; e) Rodeo locality. Abbreviations: C, Chiroptera; E, Eomyidae; I, Insectivora; LAG, Lagomorpha; M, Mustelidae; O, Other (borderline microfaunal-megafaunal taxa); PER, Perognathinae; Pf, Proheteromys floridanus; Pm, Proheteromys magnus; S, Sciuridae; S1, Sciurid species 1; S2, Sciurid species 2; Sc, Scalopus; So, Sorex; Th, Thomomys.

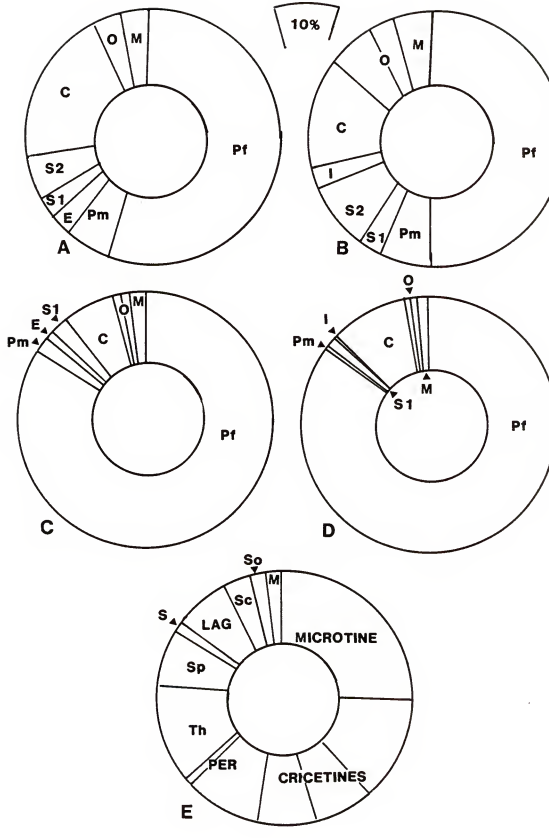

10%
O
M
C
Pf
S2
S1
E
Pm
A
O
M
C
Pf
I
S2
S1
Pm
B
S1
E
Pm
O
M
C
Pf
C
O
I
Pm
C
M
S1
Pf
D
So
M
Sc
S
LAG
MICROTINE
Sp
Th
PER
CRICETINES
E

Figure 5-7. Histograms of relative representations of skeletal elements of small mammals in modern mammalian carnivore scat compared to relative representations of Proheteromys floridanus elements from Thomas Farm. Recent data from Andrews and Nesbit Evans, 1983. a) Mongoose; b) Red fox; c) Coyote; d) Unit 15, Thomas Farm. Abbreviations: Cteeth, cheekteeth; Cal/Ast, Calcaneum and astragalus; Met, metapodial.

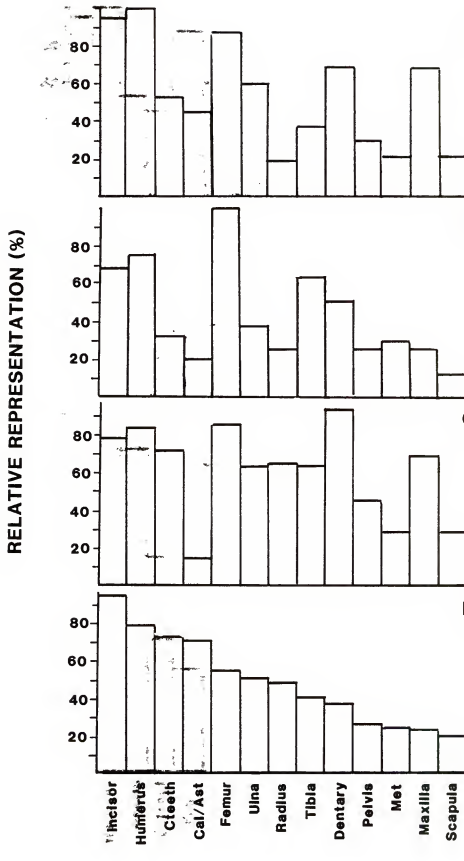

RELATIVE REPRESENTATION (%)
A
B
C
D
20
40
60
80
Incisor
Humerus
Cheek
Cal/Ast
Femur
Ulna
Radius
Tibia
Dentary
Pelvis
Met
Maxilla
Scapula

Figure 5-8. Histograms of relative representations of skeletal elements of small mammals in raptor pellets compared to relative representation of Proheteromys floridanus elements from Thomas Farm. Owl data from Korth (1979), Pratt (1979), Dodson and Wexlar (1979). a) Great horned owl; b) Barn owl c) Red-tailed hawk d) Unit 15, Thomas Farm. For list of abbreviations see Figure 5-7.

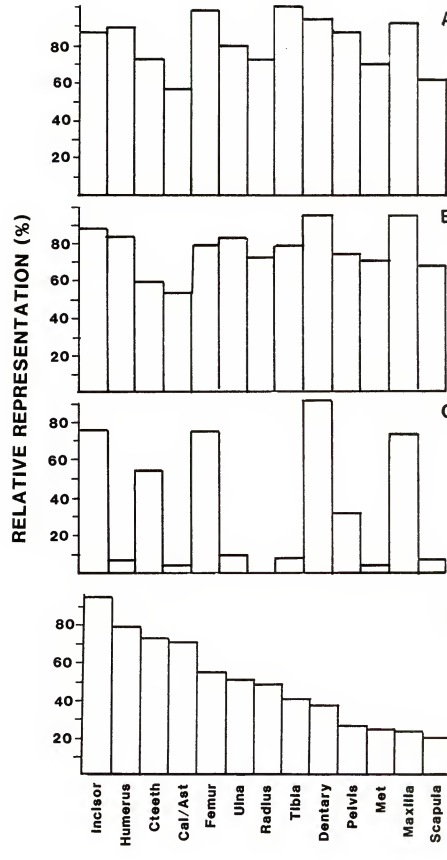

RELATIVE REPRESENTATION (%)
A
B
C
D
20
40
60
80
Incisor
Humerus
Cteeth
Cal/Ast
Femur
Ulna
Radius
Tibia
Dentary
Pelvis
Met
Maxilla
Scapula

Table 5-1. Dry weights of sediment samples used in microfaunal analysis.

Unit	Sediment Type	Dry Weight (kg)
5	sandy clay	214
6/7	clay/sandy clay	197
11	Boulders, sand	191
15	limesand	191

Table 5-2. Relative representations of skeletal elements of small mammals in coyote scat. Study 1; Korth (1979), Study 2; Andrews and Nesbit Evans (1983). Average values from both studies were used in this paper.

Element	Study 1	Study 2	Average
Maxilla	78.6	57.1	67.8
Dentary	92.5	92.8	92.6
Incisors	100.0	57.1	78.6
Cheekteeth	78.9	29.8	24.5
Scapula	45.2	14.3	29.6
Humerus	69.0	100.0	84.5
Radius	59.5	71.4	65.5
Ulna	63.1	64.3	63.5
Innominate	47.6	42.0	44.8
Femur	70.0	100.0	85.0
Tibia/fibula	48.8	85.7	67.3
Calcan./astrag.	19.0	9.0	14.0
Metatarsals		28.9	28.9
TOTAL MEAN PRESERVATION			55.8

Table 5-3. Relative abundances of microfaunal taxa from Thomas Farm.

A. UNIT 5

Taxon	Number of Specimens	Percent of total	MNI	Percent of total
Osteichthyes	4	0.4	1	0.6
Urodela	215	20.8	13	8.6
Anura	376	36.7	87	57.6
Squamata	127	12.4	17	11.2
Aves	4	0.4	3	2.0
Chiroptera	35	3.4	6	3.9
Rodentia	264	24.3	24	15.9
TOTAL	1025	100.0	151	100.0

B. UNIT 6-7

Osteichthyes	8	1.1	2	1.8
Urodela	54	8.7	5	4.5
Anura	246	39.1	54	48.6
Squamata	61	9.7	16	14.4
Aves	16	2.5	5	4.5
Chiroptera	49	7.8	5	4.5
Insectivora	3	0.5	1	0.9
Rodentia	197	31.3	23	20.7
TOTAL	634	100.0	111	100.0

C. UNIT 11

Osteichthyes	3	0.2	1	0.7
Urodela	4	0.3	1	0.7
Anura	260	15.6	46	30.5
Squamata	118	7.1	13	8.6
Aves	35	2.1	6	3.9
Chiroptera	93	5.6	6	3.9
Rodentia	1159	69.2	78	51.6
TOTAL	1672	100.0	151	100.0

D. UNIT 15

Osteichthyes	1	0.01	1	0.2
Urodela	53	0.8	5	1.2
Anura	1217	17.9	174	42.2
Squamata	412	6.1	43	10.4
Aves	51	0.8	9	2.2
Chiroptera	274	4.1	19	4.6
Insectivora	2	0.03	1	0.2
Rodentia	4776	70.2	160	38.8
TOTAL	6786	100.0	412	100.0

Table 5-4. Relative Representations of skeletal elements of *Proheteromys floridanus* from Thomas Farm.

Element	Relative Representation Unit 15	Unit 11	Unit 6/7	Unit 5
Maxilla	23.5	6.2	3.3	0.0
Dentary	36.0	10.9	3.3	2.8
Incisors	94.4	82.4	73.3	90.3
Cheekteeth	73.3	35.8	29.2	30.9
Scapula	20.7	14.4	3.3	5.5
Humerus	77.1	44.5	13.3	30.1
Radius	48.1	19.2	6.7	16.7
Ulna	50.3	24.6	13.3	25.0
Innominate	26.4	15.1	0.0	19.4
Femur	53.8	36.9	16.7	13.8
Tibia/fibula	39.2	21.9	30.0	22.2
Calcan./astrag.	70.2	39.4	26.6	26.3
Metatarsals	25.0	11.9	4.6	12.2
TOTAL MEAN PRESERVATION	49.1	27.1	17.2	21.5
STANDARD DEVIATION	22.6	20.5	19.1	21.7

Table 5-5. Relative Representations of Anuran Elements

A. Relative representations of selected anuran elements from Thomas Farm and from Cayman Islands barn owl pellets.

Element	Cayman Brac	Unit 15	Unit 11	Unit 6/7	Unit 5
Ilium	96.1	91.4	75.6	83.3	90.1
Humerus	66.6	77.6	66.3	66.3	45.5
Urostyle	37.4	68.9	50.0	46.3	39.0
Radius/ulna	36.8	89.7	75.0	32.4	31.6
Sacrum	29.8	35.1	21.7	14.8	18.4
Scapula	23.8	32.2	30.4	14.8	19.4
MEAN					
STANDARD DEV.					

B. Preservation ratios of relative representations of Thomas Farm auran elements to representations of anuran elements from barn owl pellets from the Cayman Islands.

Element	Unit 15	Unit 11	Unit 6/7	Unit 5
Ilium	0.95	0.79	0.87	0.94
Humerus	1.17	0.99	0.99	0.68
Urostyle	1.84	1.34	1.24	1.04
Radius/ulna	2.43	2.03	0.88	0.86
Sacrum	1.17	0.73	0.50	0.62
Scapula	1.35	1.28	0.62	0.82

Table 5-6. Ratios of relative representations of elements of Proheteromys floridanus from unit 15 to relative representations of elements of small mammals in predator scat and pellets. Mean values are for underrepresented elements only, S.D. is standard deviation of mean.

	Preservation ratios (unit15/predator)						
Element	Coyote	Fox	Mongoose	Barn Owl	G.H. Owl	Screech Owl	Hawk
Maxilla	0.34	0.94	0.36	0.25	0.25	0.35	0.31
Dentary	0.39	0.72	0.52	0.39	0.39	0.42	0.38
Incisors	1.19	1.36	0.98	1.09	1.08	----	1.28
Cheekteeth	1.34	2.34	1.41	1.22	1.03	----	1.15
Scapula	0.69	1.65	0.91	0.27	0.34	0.62	3.30
Humerus	0.91	1.02	0.77	0.94	0.88	1.15	12.36
Radius	0.73	1.92	2.64	0.65	0.66	0.64	*
Ulna	0.80	1.34	0.85	0.62	0.64	0.61	8.08
Innominate	0.60	1.06	0.83	0.35	0.31	0.33	0.84
Femur	0.63	0.54	0.66	0.69	0.56	0.56	0.71
Tibia	0.58	0.63	1.07	0.51	0.50	0.50	4.17
Tarsals	5.06	3.74	1.17	1.45	1.22	0.96	46.34
Metatarsals	0.86	0.87	1.22	----	----	----	20.15
MEAN (underrep.)	0.65	0.74	0.74	0.52	0.50	0.55	----
S.D.	0.18	0.15	0.19	0.21	0.19	0.18	

* denominator = 0, ratio cannot be calculated

Table 5-7. Ratios of ends of selected long bones from unit 15 and predator scat or pellets. Only broken ends are counted. Ratio = Number of one end of bone/total number of both ends of bone.

	Unit 15	Coyote	Fox	Mongoose	Barn Owl	G.H. Owl	Screech Owl	Hawk
Humerus								
No. ends	232	76	100	61	3	16	10	2
% Proximal	25	50	17	47	66	68	66	0
% Distal	75	50	83	53	33	31	22	100
Femur								
No. ends	234	92	100	76	0	19	7	26
% Proximal	68	54	67	68		32	29	92
% Distal	32	46	33	32		68	71	8
Tibia								
No. ends	172	100	100	63	5	5	3	shafts
% Proximal	37	90	67	40	20	80	33	
% Distal	63	10	33	60	80	20	67	

Table 5-8. Settling velocities, quartz grain equivalents (dq_e), and dq_e ranks for skeletal elements of Peromyscus and Rana. See text for explanation.

A. Peromyscus

Element	Settling Velocity (cm/sec)	dq_e (mm)	Rank
Maxilla (edent.)	6.87	0.44	7
Dentary (edent.)	6.36	0.38	10
Incisor	10.89	1.10	1
Cheektooth	9.96	0.87	2
Scapula (prox.)	5.41	0.27	12
Humerus (dist.)	7.63	0.54	5
Radius (prox.)	6.56	0.40	8
Ulna (prox.)	5.78	0.31	11
Ilium/acetabulum	6.54	0.39	9
Femur (prox.)	7.96	0.59	4
Tibia/fibula (dist.)	8.70	0.70	3
Calcaneum/astragalus	7.10	0.47	6
Metatarsal	4.93	0.23	13

B. Rana

Element	Settling Velocity (cm/sec)	dq_e (mm)	Rank
Scapula	4.88	0.22	6
Humerus	16.58	2.55	1
Radius/ulna	8.78	0.70	3
Urostyle	5.69	0.30	5
Ilium	10.51	1.04	2
Sacrum	5.85	0.32	4

Table 5-9. Relative representations of skeletal elements of Proheteromys floridanus from unit 15 based on expected representations of elements from carnivore scat, and quartz grain equivalent ranks.

A. Relative abundance rank corrected for coyote scat		dq_e rank
1. Calcaneum/astrag.		6
2. Cheekteeth	>100	2
3. Incisor		1
4. Humerus	> 90	5
5. Metatarsal	> 80	13
6. Ulna		11
7. Radius	> 70	8
8. Femur		4
9. Scapula	> 60	12
10. Pelvis		9
11. Tibia	> 50	3
12. Dentary		10
13. Maxilla	> 30	7

B. Relative abundance rank corrected for fox scat		dq_e rank
1. Calcaneum/astrag.		6
2. Cheekteeth		2
3. Radius	>100	8
4. Scapula		12
5. Incisor		1
6. Ulna		11
7. Pelvis		9
8. Humerus		5
9. Maxilla	> 90	7
10. Metatarsal	> 80	13
11. Dentary	> 70	10
12. Tibia	> 60	3
13. Femur	> 50	4

D. Relative abundance rank corrected for mongoose scat		dq_e rank
1. Radius		8
2. Calcaneum/astrag.		6
3. Cheekteeth	>100	2
4. Metatarsal		13
5. Tibia		3
6. Incisor	> 90	1
7. Scapula		12
8. Ulna		11
9. Pelvis	> 80	9
10. Humerus	> 70	5
12. Femur	> 60	4
13. Dentary	> 50	10
14. Maxilla	> 30	7

Table 5-10. Relative representations of skeletal elements of Proheteromys floridanus from unit 15 based on expected representations of elements from raptor pellets, and quartz grain equivalent ranks.

A. Relative abundance ranks based on barn owl pellets		dq_e rank
1. Calcaneum/astragalus		6
2. Cheekteeth		2
3. Incisors		1
4. Humerus	> 90	5
6. Femur		4
7. Radius	> 60	8
8. Ulna		11
9. Tibia	> 50	3
10. Dentary		10
11. Pelvis	> 30	9
12. Scapula		12
13. Maxilla	> 20	7

B. Relative abundance ranks based on G.H. owl pellets		dq_e rank
1. Calcaneum/astragalus		6
2. Incisors	>100	1
3. Cheekteeth		2
4. Humerus	> 80	5
5. Radius	> 60	8
6. Ulna		11
7. Femur	> 50	4
8. Tibia		3
9. Dentary		10
10. Scapula	> 30	12
11. Pelvis		9
12. Maxilla	> 20	7

C. Relative abundance rank based on screech owl pellets		dq_e rank
1. Humerus	>100	5
2. Calcaneum/astragalus		6
3. Incisor	> 90	1
4. Cheekteeth	> 70	2
5. Radius		8
6. Scapula	> 60	12
7. Ulna		11
8. Femur		5
9. Tibia	> 50	3
10. Dentary	> 40	10
11. Maxilla		7
12. Pelvis	> 30	9

D. Relative abundance rank based on hawk pellets		dq_e rank
1. Calcaneum/astrag.		6
2. Metatarsal		13
3. Radius		8
4. Humerus		5
5. Ulna	>100	11
6. Tibia		3
7. Scapula		12
8. Incisor		1
9. Cheekteeth		2
10. Pelvis	> 80	9
11. Femur	> 70	4
12. Dentary	> 30	10
13. Maxilla		7

Table 5-11. Relative representations of skeletal elements of Proheteromys floridanus from units 5 through 11 based on expected representations of elements from unit 15 and quartz grain equivalent ranks.

A. UNIT 11 Element	corrected % pres.	dq_e rank
1. Incisors	87.3	1
2. Scapula	69.6	12
3. Femur	68.6	4
4. Humerus	57.9	5
5. Pelvis	57.3	9
6. Calcan/astrag.	55.9	6
7. Tibia	53.8	3
8. Ulna	44.9	11
9. Cheekteeth	45.9	2
10. Metatarsal	47.6	13
11. Radius	39.9	8
12. Dentary	30.3	10
13. Maxilla	26.2	7

B. UNIT 6/7 Element	corrected % pres.	dq_e rank
1. Incisors	77.4	1
2. Tibia	76.5	3
3. Cheekteeth	40.0	2
4. Calcan/astrag.	37.8	6
5. Femur	31.3	4
6. Ulna	26.5	11
7. Metatarsal	18.4	13
8. Humerus	17.3	5
9. Scapula	15.9	12
10. Maxilla	14.1	7
11. Radius	13.9	8
12. Dentary	9.2	10
13. Pelvis	0.0	9

C.UNIT 5 Element	corrected % pres.	d_e rank
1. Incisors	95.0	1
2. Pelvis	74.0	9
3. Tibia	56.6	3
4. Ulna	49.8	11
5. Metatarsal	49.2	13
6. Cheekteeth	42.2	2
7. Humerus	39.8	5
8. Calcan/astrag.	37.4	6
9. Radius	34.7	8
10. Scapula	26.6	12
11. Femur	25.7	4
12. Dentary	7.8	10
13. Maxilla	0.0	7

Table 5-12. Relative representations of elements of Proheteromys floridanus and quartz grain equivalent ranks.

A. UNIT 15

Element	Relative Represent.	dq_e rank
1. Incisors	> 90	1
2. Humerus		5
3. Cheekteeth	> 70	2
4. Calcan/astrag.		6
5. Femur	> 50	4
6. Ulna		11
7. Radius	> 40	8
8. Tibia	> 30	3
9. Dentary		10
10. Pelvis		9
11. Metatarsal	> 20	13
12. Maxilla		7
13. Scapula		12

B. UNIT 11

Element	Relative Represent.	dq_e rank
1. Incisors	> 80	1
2. Humerus	> 40	5
3. Calcan/astrag.		6
4. Femur	> 30	4
5. Cheekteeth		2
6. Ulna	> 20	11
7. Tibia		3
8. Radius		8
9. Pelvis		9
10. Scapula	> 10	12
11. Metatarsal		13
12. Dentary		10
13. Maxilla	> 0	7

C. UNIT 6/7

Element	Relative Represent.	dq_e rank
1. Incisors	> 70	1
2. Tibia	> 30	3
3. Cheekteeth	> 20	2
5. Calcan/astrag.		6
5. Femur		4
6. Humerus	> 10	5
7. Ulna		11
8. Radius		8
9. Metatarsal		13
10. Maxilla	> 0	7
11. Scapula		12
12. Dentary		10
13. Pelvis	0	9

D. UNIT 5

Element	Relative Represent.	dq_e rank
1. Incisors	> 90	1
2. Cheekteeth	> 30	2
3. Humerus		5
4. Calcan/astrag.		6
5. Ulna	> 20	11
6. Tibia		3
7. Pelvis		9
8. Radius	> 10	8
9. Femur		4
10. Metatarsal		13
11. Scapula	> 0	12
12. Dentary		10
13. Maxilla	0	7

Table 5-13. Relative representations of anuran elements from Thomas Farm, and quartz grain equivalent rank.

A. UNIT 15

Element	Relative Represent.	dq_e rank
1. Ilium	> 90	2
2. Rad/ulna	> 80	3
3. Humerus	> 70	1
4. Urostyle	> 60	5
5. Sacrum	> 30	4
6. Scapula		6

B. UNIT 11

Element	Relative Represent.	dq_e rank
1. Ulna	> 70	3
2. Ilium		2
3. Humerus	> 60	1
4. Urostyle	> 50	5
5. Scapula	> 30	6
6. Sacrum	> 20	4

C. UNIT 6/7

1. Ilium	> 80	2
2. Humerus	> 60	1
3. Urostyle	> 40	5
4. Rad/ulna	> 30	3
5. Sacrum	> 10	4
6. Scapula		6

1. Ilium	> 90	2
2. Humerus	> 40	1
3. Urostyle	> 30	5
4. Rad/ulna		3
5. Scapula	> 10	6
6. Sacrum		4

CHAPTER 6
HERPETOFAUNA PALEOECOLOGY

The Thomas Farm possesses an extensive amphibian and reptilian fauna. Within the Amphibia, urodeles are relatively uncommon, both in number of species and numbers of individuals. The anuran fauna is large, and several papers have been published on this portion of the herpetofauna (Tihen, 1951; Auffenberg, 1956; Holman, 1961, 1965, 1967). Anuran remains are also relatively easy to identify based on the morphology of the ilium. Because frogs and toads at Thomas Farm form a major portion of the vertebrate fauna, the Anura has been treated in a rather extensive paleoecological analysis in this chapter. The other members of the herpetofauna are not as well known, as abundant, nor as easy to identify, and they will not be considered in great detail at this time.

Amphibia

Anura

Sixteen species of amphibians have been reported from Thomas Farm, the majority of which are anurans (Tihen, 1951; Auffenberg, 1956; Holman, 1961, 1965; Estes, 1963). This diverse anuran fauna is well suited to paleoecological analysis. Detailed analysis of a group such as anurans entails the comparison of fossil forms with recent relatives or ecomorphs, and is most informative when the modern counterparts of the taxa being studied exhibit fairly specific habitat preferences; however, inferences concerning habitats of a particular type of frog must be made with caution. Regardless of the environment

in which a frog is found most of the year, with very few exceptions it must return to water to reproduce (Duellman and Trueb, 1986). Breeding ponds may be used by several species of frogs simultaneously (Wiest, 1982). A fossil deposit formed under aquatic conditions could hypothetically contain a variety of species, each indicative of a different habitat type. It is therefore critical to be able to distinguish breeding aggregations from resident populations in a fossil locality.

The analysis of the Thomas Farm anurans was based on ilia for several reasons. First, the ilium is one of the most diagnostic bones in a frog skeleton, and is identifiable to the species level. A number of the frogs from Thomas Farm have been described on the basis of this element (Tihen, 1951; Auffenberg, 1956; Holman, 1961, 1965, 1967; Lynch, 1971). Second, the ilia are the most abundant anuran elements represented at Thomas Farm, and were used in MNI determinations. Third, the measurement of the height of the acetabulum is a reliable indicator of body size (Chapter 2, p. 24).

Anuran families at the Thomas Farm locality represented by the largest number of individuals (the Bufonidae, Hylidae, and Ranidae) will be considered most extensively in this analysis. The population dynamics of the major families will be examined first, and the amphibian fauna from the entire site will then be discussed.

Bufonidae. Bufonids are the most abundant anurans in terms of numbers of individuals found at Thomas Farm, dominating the amphibian fauna in all levels except unit 5. Only one species, Bufo praevius, has been named (Tihen, 1951). Other workers have examined the large number of bufonid specimens from the locality and have agreed that

only one species of the genus Bufo is represented (Auffenberg, 1956; Holman, 1961). Recently collected material is also assignable to this species. While Tihen (1951) stated that the affinities of the Thomas Farm bufonid were with the West Indian radiation of the Bufo valliceps group (now considered a separate genus Peltophryne by Pregill, 1981), Auffenberg (1956) felt that the species was closest to the North American Bufo woodhousei-terrestris group.

Ilia examined in this study were obtained from the four randomly collected 200-kg matrix samples discussed in Chapter 2 and 5. Specimens complete enough to provide accurate acetabular height measurements were measured as described in Chapter 2 (p. 25). Material collected from other matrix samples was also examined in an effort to locate the largest and smallest ilia of each species, however, all the additional ilia measured fell within the size range of those collected in the comparative samples.

The largest and smallest acetabular height measurements for the species were converted to snout-vent length measurements by referring to the regression equation shown in Figure 6-1. The regression for bufonids was based on measurements of 22 recent bufonids representing 7 species (Table 6-1). Estimated size ranges of Bufo praevius from each sedimentary unit are compared with post-metamorphic size ranges of Recent species in Figure 6-2 (data from Wright and Wright, 1949, and Conant, 1975). Recent species selected for comparison either occur in Florida today, or have been named as close relatives of the fossil form (Tihen, 1951; Auffenberg, 1956). The size ranges of the recent frogs have been divided into average juvenile and adult size ranges based on descriptions in Wright and Wright (1949). The size

range estimate for Bufo praevius calculated from the fossil ilia may or may not reflect the actual size range of the living species. It is possible that remains of large individuals are absent, or that individuals at the lower end of the size distribution are not represented.

The small sizes of the fossil forms could lead one to assume that the fossil bufonids represented are all juveniles, particularly when the sizes of the fossil Bufo are compared with those of large bufonids such as Bufo valliceps or B. woodhousei. Population assemblages composed predominantly of juvenile individuals have been reported (Tester and Breckenridge, 1964) and herpetologists have long known that juvenile and adult frogs of one species may frequent different habitats (Tester and Breckenridge, 1964; Blair, 1953). However, the degree of separation between immature frogs and adults is not so complete that no adults would be found in a region where juveniles are present (Tester and Breckenridge, 1964). It is also unlikely, given the hundreds of specimens of Bufo praevius from Thomas Farm, that no large adults would be represented. Another line of evidence comes from examination of the condition of the fossil bone. Juvenile frog ilia possess numerous perforations in the bone that are not seen on adult ilia (Holman, 1965). The majority of ilia of Bufo praevius do not show this characteristic, and therefore probably were not from juvenile animals.

Conversely, it is possible that very young individuals at the lower end of the size scale are not represented. The smallest fossil bufonid ilium found in the Thomas Farm microfauna belonged to a frog that is estimated to have possessed a snout-vent length of about 22

mm. Minimum transformation sizes (stage at which a tadpole becomes a frog) for recent bufonids, even large ones, range from 7 to 12 mm, with a mean of about 8.6 mm. Most bufonids, regardless of adult size, are characterized by small size at transformation (Wright and Wright, 1949). It is highly likely that the minimum size of Bufo praevius should be extended to 8.6 mm. The absence of the smallest individuals may reflect their absence within the locality, or may indicate a sampling problem. Fossil ilia of small size are extremely fragile, and are often too fragmentary to allow for specific identification. If badly broken, a small Bufo praevius ilium could pass through even the finest screen used in this study. Further discussion concerning the significance of the absence of the extremely small bufonids will be included below. The conclusion drawn at this point is that the body lengths of individuals in a living population of Bufo praevius ranged from about 9 to 64 mm.

Population studies on recent bufonids in the wild have entailed measuring and marking large numbers of individuals and recapturing and measuring them at at regular intervals (Blair, 1943, 1953; Raney and Lachner, 1947; Hamilton 1955; Tester and Breckenridge 1964; Kelleher and Tester, 1969; Clarke, 1974, 1977). These studies, the most extensive of which monitored population changes over a seven-year period (Kelleher and Tester, 1969), provide infomation on anuran growth rates, population structure, survivorship, and behavior.

Using these data, some workers have attempted to define age classes based on snout-vent lengths (Turner, 1960a; Clarke, 1977), but others have stated that use of snout-vent lengths to determine yearly age is subject to error for a number of reasons. First, although

frogs do exhibit indeterminate growth, growth rates throughout life are not constant (Blair, 1953; Hamilton, 1955; Raney and Lachner, 1947; Tester and Breckenridge, 1964; Clarke, 1977). Bufonids grow rapidly during the first two years of life, after which the rate of growth slows considerably. Within a given age class, growth rates may be more rapid for females than for males (Tester and Breckenridge, 1964; Brown and Alcala 1970), although males may attain sexual maturity a full season (year) before females (Raney and Lachner, 1947; Blair, 1953). The length of breeding season also determines in part the size variation within a given age class. Juveniles hatched and transformed early in the season have the potential for greater growth than those juveniles that hatch and undergo metamorphosis near the end of the season. Succh variation is not as pronounced among anurans such as bufonids that are primarily explosive breeders and have one fairly short breeding bout in the spring (Wright and Wright, 1949; Crump, 1982; Duellman and Trueb, 1986).

Despite the variation in population parameters within the genus Bufo it is possible to make some generalizations that can be used to analyze the population structure of fossil bufonids. Although yearly age classes are difficult to determine, frog populations can be divided into two age classes, juveniles and adults. Juveniles are defined as individuals that have undergone metamorphosis but have not become sexually mature; adults are sexually mature individuals. The minute oak toad, Bufo quercicus, gains 11 cm, or 55% of its total possible length between metamorphosis and the end of the first growth season (Table 6-2). This frog participates in breeding the following spring, and grows to 95% of its maximum possible length by the end of

this year. Individuals seldom survive more than two years (Hamilton, 1955; Turner, 1960a). Larger bufonids show variability in the length of time required to reach sexual maturity. The Manitoba toad Bufo hemiophrys can grow between 2-21 mm within the first season, showing an average gain of 11 mm or 20% of maximum possible post-metamorphic length gain (Table 6-2). By the end of the first year after metamorphosis, these frogs have gained nearly 60% of the possible maximum length. Sexual maturity is reached either during this year or at the start of the following year (Tester and Breckenridge, 1964). Bufo hemiophrys may live more than four years, growing at a much reduced rate after the second year.

Populations of Bufo terrestris from New York (Raney and Lachner 1947; Turner, 1960a) also gain about 20% of their maximum length within the first season, and 57% in the year following transformation (Turner, 1960a; Table 6-2). The literature is unclear as to the timing of sexual maturation. Raney and Lachner (1947) state that Bufo terrestris participates in breeding choruses at two years of age; however, the size of adult Bufo terrestris, as described by Raney and Lachner (1947), falls within the range seen in the first year of growth after metamorphosis. It is possible that this toad, like B. hemiophrys, reaches maturity within this time but does not participate in breeding until the following year. A Texas population of the Mexican toad Bufo valliceps (Blair, 1953) acquires 61% of maximum growth by the end of the first year after transformation. During this season, males reach sexual maturity, but females do not become mature until the following year. No data are available on the sizes of individuals at the end of the transformation year.

Even though the growth rates and ages at which sexual maturity is attained are variable in the above species, there are some consistent patterns pertaining to age and amount of growth. After metamorphosis at about 10 mm, the larger bufonids gain about 20% of their total maximum length by the end of the first season. There also seems to be a relationship between size, if not age, at which sexual maturity is reached. All of the bufonids discussed above become adults by the time they gain 55% to 61% of their maximum possible growth (average 58%).

The calculated age-size classes for Bufo praevius are illustrated in the frequency size distributions in Figure 6-3. Acetabular heights of ilia from each unit are shown. Individuals that had gained over 58% of total estimated post-metamorphic length were considered to be adults (acetabular height of more than 2.15 mm). Differences in the distribution of bufonid sizes between levels might indicate that the population being sampled in one layer was distinctly different from that in another layer. In Figure 6-3, it can be seen that the nearly the entire known size range of Bufo praevius ilia is represented in each layer. The mean size of ilia represented ranges from 1.95 mm in unit 5 to 2.15 mm in unit 15, and one-way analysis of variance shows these means are not significantly different. The proportion of juveniles to adults is also very similar in all layers (Figure 6-3). For these reasons, I assume that the dynamics of the populations sampled in various levels were not significantly different. Combining measured specimens from all layers and converting ilial measurements to snout-vent lenths (in increments of 5mm) results in the histogram shown in Figure 6-4.

Although size-frequency histograms are used in paleoecological analysis of fossil mammals to determine whether an assemblage was formed by attrition or by a catastrophic event (Voorhies, 1969; Shipman, 1981), size-frequency distributions cannot provide such information for amphibian assemblages. A survivorship curve for bufonids (Kelleher and Tester, 1969) that is probably representative of most frog populations is shown in Figure 6-5. Greatest mortality occurs in the tadpole and early post-metamorphic juvenile stage. Estimates of percent survival of bufonids in these stages ranges from 0 to 11% (Blair, 1953; Crump, 1982; Duellman and Trueb, 1986). Succeeding age classes suffer a constant rate of mortality, estimates of which range from 80% (Clarke, 1977) to 70% yearly (Kelleher and Tester, 1969). The shape of a size-frequency histogram that reflects catastrophic death of an anuran population therefore is not clearly different from that of an attritional assemblage.

Comparisons of the size-frequency histogram of Bufo praevius with size-frequency histograms of living frog populations (Tester and Breckenridge, 1964; Raney and Lachner, 1947; Figure 6-6) indicates possible population structure and habitat of the fossil form. The size distribution of frogs in the fossil assemblage does not clearly resemble that seen in any of the representative living populations, although it shares some similarities with the size-frequency histogram of a resident population of Bufo hemiophrys censused as the frogs emerged from their winter hibernacula (Tester and Breckenridge, 1964). In both the populations, individuals in the 10-20 mm size class are absent. Their absence in the modern population is clearly a function of the time of year when the frogs were sampled. The census

was taken prior to breeding season, so the youngest (smallest) frogs present were those that had metamorphosed during the previous summer and had grown about 10 mm during that season. The lack of very small Bufo praevius may indicate the members of the population in the region of the site were being deposited at a time of year when no small juveniles were present. The absence of very small bufonids may also be related to the behavior patterns of newly metamorphosed frogs. Very young bufonids tend to remain near the breeding site for their entire first season, long after adults have moved away from the area (Clarke, 1974; Raney and Lachner, 1947). The lack of very small frogs therefore suggests that bufonids were not actively breeding at the sinkhole (possibly because of water depth, or inaccessibility, among other factors), but were mating at nearby other locations. The possibility that the absence of small individuals is a function of preservation or sampling biases cannot be ignored. Skeletal elements of young frogs are for the most part cartilaginous, and as such would not be preserved (Duellman and Trueb, 1986; R. Franz, pers. comm). Small ilia of very young frogs could also be missed in matrix sorting.

Although the Bufo hemiophrys size-frequency histogram (Tester and Breckenridge, 1964) resembles that of Bufo praevius in the absence of very small individuals, it differs in terms of abundance of first-year juveniles. The modern population was censused the year after a highly successful breeding season and very mild winter (Tester and Breckenridge, 1964). Juveniles accounted for 93% of the entire population, although this ratio has been shown to vary yearly. During the seven years in which the study on B. hemiophrys was conducted, the percentage of juveniles in the population ranged from 60% to 93%, with

an average of 76% (Kelleher and Tester, 1969). The percentage of juveniles in the fossil assemblage is 48% if the numerous 40-45 mm individuals are included with the adults, and rises to 70% if the individuals in this group are counted as juveniles. Given the variation in size at sexual maturity, it is probably more reasonable to consider half of the individuals in this particular size class as juveniles and half as adults. The ratio of numbers of juveniles in the sample of fossil bufonids would then be 58%.

The second type of size distribution of a recent population is that of a breeding aggregation. A representative size-frequency histogram of a breeding population of Bufo terrestris (Raney and Lachner, 1947) is illustrated in Figure 6-6. The smallest size class is absent, as no frogs of this size are present during the most of the breeding season. Larger (non-breeding) juveniles are also very rare, representing only about 8% of the total population. The differences between this size distribution and the fossil assemblage suggests that the Thomas Farm bufonids were not merely using the site as a breeding locality.

Conclusions that may be drawn concerning Bufo praevius at Thomas Farm are as follows;

1. The shape of the frequency-size histogram for the fossil bufonid is most similar to that of a resident population of Bufo. The similarity of size ranges and mean sizes between layers indicates that population structure was not significantly different between these layers, and that a resident population was being sampled.

2. The absence of very small individuals may be related to the life history of the frog, taphonomic factors affecting the assemblage prior to deposition, sampling bias, or a combination of these factors.

3. The lack of presumably newly metamorphosed individuals, coupled with the differences between the fossil frequency-size histogram and a breeding aggregation histogram may indicate that bufonids were not using the locality itself as a breeding ground. The presence of large numbers of bufonids indicates that suitable conditions for breeding were nearby.

4. The large number of bufonids in unit 15 may have been accumulated by a carnivore. Several mammalian predators are known to feed on bufonids (Ewer, 1973), including raccoons (Clarke, 1977) and badgers (Tester and Breckenridge, 1964). Some birds of prey (kites), also feed primarily on frogs. The shape of the size-frequency histogram of bufonids from unit 15 may reflect sizes of frogs selected by a predator. Small toads may be absent as their bones would be totally digested by a predator.

Hylids. Several species of hylid are known from Thomas Farm. Auffenberg (1956) described the extinct species Hyla goini, which Holman(1967) later stated was closely related to Hyla femoralis and Hyla squirrela. Holman also described a new hylid species, Hyla miofloridana (1967). My examination of the most recently collected material indicates that a third, as yet unnamed species of Hyla is also present. The majority the hylid ilia found in the course of this study are referrable to Hyla goini.

The small hylid Acris barbouri was described by Holman (1967), who placed this frog near the ancestry of the Acris crepitans - gryllus group. He also named the new genus Proacris mintoni (1961). Specimens of this tiny hylid are rare. The presence of a large number of hylid frogs is just one of the many unusual features of the Thomas Farm locality. Tree frogs are rare in most fossil localities (Lynch, 1962).

Size ranges of selected North American members of the genus Hyla (data from Wright and Wright, 1949, and Conant, 1975) are compared with the estimated size range of Hyla goini from the Thomas Farm (Figure 6-7). Snout-vent lengths of the fossil form were calculated from iliial acetabular heights using the regression equation for hylids shown in Figure 6-8. The size range of Hyla goini falls within the range of most other species shown, and is closest to that of Hyla andersoni and Hyla versicolor. Small individuals of the fossil form appear to be underrepresented in the samples. The mean transformation size for the modern hylids shown in Figure 6-7 is 11.4 mm. The smallest estimated size of the fossil form is 19 mm. The lack of small individuals may be due to any of the factors discussed previously for bufonids to account for the lack of small bufonids.

Relatively few population ecology studies have been conducted on hylids, possibly because members of this group are more difficult to track than bufonids. Jameson (1956) investigated growth rates, age structure, and survivorship of a population of Hyla regilla. He found that newly transformed frogs (average transformation size 13.8 mm) grew rapidly until the end of the first season. Although he recovered only two individuals of this age class at the beginning of the

following year, they each showed a gain in length of over 17 mm (a gain of 50% of maximum possible length) and were participating in breeding. By the end of the first year following transformation, these individuals measured over 35 mm, a gain of over 60% of the maximum growth. Jameson found that individuals over 35 mm in length were relatively rare. He attributed this lower representation to predation on these larger, more obvious members of the population. It is also possible that the life span of this frog in most cases is no longer than two years.

Jameson's data on the size at which sexual maturity is attained in Hyla regilla are compared with the average sizes of juvenile and adult age classes listed in Wright and Wright (1949). Table 6-3 shows the average length of juvenile size gain in each species divided by the maximum possible gain. This percentage ranges from 38% to 64% with a mean of 47%. The figure is close to that found by Jameson for size at the start of the first year following transformation (a gain of 50% of maximum possible).

Using the 50% figure as an estimate for the relative size at maturity, adults of Hyla goini are defined as greater than 31 mm in length. Histograms of ilium size in Figure 6-9 show the ratios of juveniles to adults in the various sediment levels. In units 11 and 15, the ratios of juveniles to adults are similar, with about equal numbers in each of the two major classes. These ratios are different from those seen in Units 6-7 and unit 5, where juveniles represent over 75% of the specimens. The difference in the size structure of the populations may be interpreted in several ways. The hylids represented Unit 15 may have been eaten by a predator, as has been

discussed previously, and smaller individuals either were not eaten, or their skeletal elements did not survive digestion. The higher proportion of juveniles in Unit 5 could indicate that this portion of the site served as a breeding locality for Hyla. There is some data showing that young hylids remain near the pond from which they hatched until the end of their first season of life (Jameson, 1956). It would be expected, given the low survivorship of this group (Jameson, 1956; Duellman and Trueb, 1986), that large numbers of juvenile individuals would die near the sinkhole, if breeding had taken place there. Larger samples of Hyla from the various layers are needed before this question can be answered.

The next most common hylid found at the Thomas Farm site is the fossil cricket frog, Acris barbouri. The calculated snout-vent size range based on ilia indicates that this frog was even smaller than recent species of Acris (Figure 6-7), however, sample sizes of this frog are too low to definitely state that such is the case. Little information is available on age-size classes of cricket frogs, although Pyburn (1958) found that Acris gryllus grows very rapidly in its first year of life, attaining sexual maturity in the same summer that it metamorphoses. No hypotheses can be formed concerning the population structure of Acris barbouri represented within the various levels (Figure 6-10), although the presence of very small individuals in unit 6-7 may indicate that a breeding population was present in the area at the time this unit was deposited. The larger numbers of this frog in unit 5 relative to its abundance in other layers was mentioned earlier (Chapters 3 and 5) as support for this layer being formed under aquatic conditions. Living species of Acris are most often

found in or around ponds or streams (Wright and Wright, 1949; Pyburn, 1958; Turner, 1960a; Conant, 1975, Duellman and Trueb, 1986).

Ranids. The Thomas Farm ranids are in need of systematic revision. The most common ranid found at the locality was orginally described by Holman (1965) as a leptodactylid, Leptodactylus abavus. Lynch (1971) disagreed with this assignment, stating that the ilial morphology of this frog indicated it should be reassigned to the genus Rana.

Other ranids described by Holman (1965, 1967) include Rana miocenica, the description of which was based on one large ilium. Unfortunately, no additional material of this species has been found. Holman also described Rana bucella on the basis of one ilium (1965). This frog, although rare, is now represented by several other specimens and does appear to be a valid species. In 1965, Holman referred three ilia from Thomas Farm to the living species Rana pipiens. Examination of these specimens shows that the smallest belongs to the taxon orignally described as Leptodactylus abavus. The two other specimens may be Rana pipiens or a closely related form, or may be small individuals of Rana miocenica. Because relatively few of these larger ranid specimens are known from the Thomas Farm, their identification remains unresolved.

The minute Rana abava (Lynch, 1971) is the most common ranid and the ilia are clearly distinguishable from those of the larger described forms. The known size range of Rana abava, based on the acetabular height regression for ranids (Figure 6-11) is compared with size ranges of selected recent ranids (Figure 6-12). The size range of this frog is considerably smaller than that of any other North

American ranid, and for this reason the possibility that the fossil ranids were all juveniles must be considered. Comparison of the smallest estimated size of Rana abava with the smallest transformed size of recent ranids (Figure 6-12) indicates that these forms are too small to be newly transformed individuals of a large ranid. Within the family Ranidae, transformation size increases as maximum adult size increases (Wright and Wright, 1949). Ranids with transformation sizes similar to the minimum size of Rana abava do not exceed 60 mm in adult snout-vent length. Therefore, it is likely that the size range of Rana abava shown in Figure 6-11 reflects the actual juvenile to adult size range of the living frog.

Numerous studies on ranid population ecology have been conducted. The majority of species investigated are north-temperate forms (Raney and Ingram, 1941; Ryan, 1953; Martof, 1956a, b; Turner, 1958, 1960b), although a few tropical ranids have also been observed (Inger and Greenberg, 1966; Brown and Alcala, 1970). It is difficult to make any generalizations concerning population structure of fossil ranids because a great deal of variation is seen in the population ecology and life history strategies of recent ranids. Tropical ranids grow rapidly and attain sexual maturity early in life (Brown and Alcala, 1970) while temperate forms grow more slowly and reach maturity after several years (Turner, 1960b). Brown and Alcala (1970) have shown that females of the Philippine ranid Rana erythrea grow at a more rapid rate than do males, and that growth for both sexes occurs throughout the year, unlike growth of more temperate forms that slows in the winter (Turner, 1960b; Martof, 1956a, b). Age classes are less well-defined in ranids than in bufonids, as the breeding season is

lengthy, and young may transform at any time during the breeding season. A given age class is composed of larger individuals that metamorphosed early in the year, and smaller individuals that transformed later in the season.

One feature that shows relatively little variation regardless of the type of ranid under consideration is the amount of growth (relative to maximum adult growth) at which an individual attains maturity. Tropical forms reach adulthood when approximately 55-60% of maximum possible growth has been reached (Inger and Greenberg, 1966; Brown and Alcala, 1970), while temperate species usually gain about 70% of their maximum length before partipating in breeding (Turner, 1960b). Even allowing for the variation described above, it is possible to divide a fossil ranid population into juvenile and adult size classes. In this study, individuals were considered juveniles if their calculated snout-vent length gain after transformation was less than 60% of the maximum possible gain (actual length of up to 35 mm).

The histograms in Figure 6-13 show the size ranges of Rana abava ilia from the various samples. In unit 15, very small individuals are absent, and juveniles represent about 66% of the sample. Only one specimen of Rana abava was found in unit 11. The ranid is most common in unit 5 and 80% of the specimens from this unit appear to be juveniles. A histogram of predicted sizes of Rana abava from unit 5 is shown in Figure 6-14. The proposed preferred habitat of Rana abava simplifies the analysis of population structure. Ranids that frequent aquatic habitats and are strong swimmers have a characteristic ilial morphology. Rana abava ilia possess many of these features (Pratt, in prep.), and I hypothesize that these ranids were primarily water-

dwellers. Some aquatic ranid species remain at the pond where they were hatched (Ryan 1953). Brown and Alcala (1970) found that in a resident population of Rana erythrea, juveniles formed between 70 to 85% of the population. This ratio is close to that seen in unit 5 and unit 6-7, although the sample size from the latter unit is small. I suggest, based on the presumed aquatic habitat favored by R. abava, and the similarity of the frequency-size histogram of ranids in unit 5 to that of a resident population of modern ranids, that the fossil form was living and breeding in the sinkhole at the time that unit 5 was deposited. However, the presence of Rana abava in unit 15 does not necessarily indicate that this portion of the deposit was formed under aquatic conditions. The proportion of juveniles in unit 15 is lower than that of a resident population. The absence of very small individuals in this level is probaly not an artifact, as they are present in other levels of the site. The third line of evidence is provided by the relative numbers of frogs, discussed previously in Chapter 2. Although a fair number of individuals of Rana abava occur in unit 15, they form only a small proportion of the entire anuran sample in this level, which is dominated by Bufo praevius. It is possible that many of the anurans found in this level were deposited by mammalian or avian carnivores that hunted in the region. Ranids are subject to predation by a wide range of animals (Martof, 1956a, b).

Community Analysis of the Thomas Farm Anurans

The remainder of this section is an analysis of the anuran community at the Thomas Farm locality. The samples from each layer have been combined to provide the abundance figures shown in Table 6-

4. I feel that this procedure is justified, as all matrix samples are approximately the same weight and all were obtained randomly. Although different depositional regimes and microhabitats may be represented within the various sedimentary samples, the species of frogs found from the lowest to the highest layer are the same. The previous discussion has shown that the frogs present within the layers were members of resident populations that no doubt were living in close proximity to the sinkhole. Combining samples from each level results in a large sample of anurans.

Table 6-4 shows the species of anurans from Thomas Farm and their relative abundances based on MNI. The family Leptodactylidae, considered by Holman to be present at the locality (Holman 1963, 1967), is not included. Leptodactylus abavus is actually a ranid (Lynch 1971, and also previous discussion), and the ilium referred to Eleutherodactylus by Holman (1967) is actually too fragmentary to be identified with certainty. No ilia assignable to Eleutherodactylus have been found in the recent excavation, and until more specimens are found, it is assumed that leptodactylids were not present in the Miocene of Florida. The ranid Rana miocenica and the microhylid Gastrophryne cf. carolinensis are included in the analysis. No specimens of these taxa were found in the random samples, but their presence in other samples indicates that they should be included in this discussion.

Community analysis of fossil forms is never as complete as an analysis of a recent community. There are many parameters that cannot be investigated due to lack of information. Anuran species diversity and resource partitioning will be discussed, and the faunal composition

of the fossil locality compared with that of a recent anuran community. Density computations cannot be made for a number of reasons, the most obvious being the lack of recent studies on anuran density that may be used for reference.

Species diversity. Species diversity indices have been criticised recently (Peet, 1975; Heatwole, 1982) as meaningless because they combine two separate entities, richness (number of species), and equitability (number of individuals in a species). Many of the newer studies on recent herpetological communities deal with these two concepts separately. This practice will be followed in this study.

Species richness. The numbers of anuran species within communities have been correlated with a number of environmental gradients. It has been shown that with decreasing latitude, the number of species in a given habitat increases (Heatwole, 1982; Duellman and Trueb, 1986). The numbers of anuran species in the tropics are therefore greater than those within temperate zones. Knowledge of the number of species within an environment permits one to make a very general estimate of latitude from which the sample was taken. The number of species of amphibians has also been shown to increase along altitudinal gradients (Heatwole, 1982; Duellman and Trueb, 1986), increasing moisture gradients, and with increasing habitat complexity. Numbers of species decrease with increasing insularity. These observations are generalities, and there is much variation in these correlations.

Of 14 species of amphibians present at the site, 11 are frogs. The number compares well with the number of frogs found in specific

habitats in Texas (Wiest, 1982), Florida (Campbell and Christman, 1982), and North Carolina (Bennett, Gibbons and Glanville, 1980). This number of species indicates the climate may have been similar to that found in Southern temperate regions today. Northern faunas may have as many as 10 species of amphibians, but the faunas are dominated by salamanders, which are more abundant than frogs in north-temperate regions (Duellman and Trueb, 1986).

The relationship between the number of (litter-dwelling) amphibian species and the number of dry months in a year (Scott, 1976; Heatwole, 1982) indicates that the region around Thomas Farm in the Miocene was probably no dryer than it is today, averaging about 5 dry months a year. The idea that has tentatively been proposed that conditions in the Florida Miocene were very dry, based on the presence of animals at the Thomas Farm locality known today to be present in dry environments (Romer, 1948; Estes, 1963) is not supported. Very xeric environments are characterized by low species richness (4 or 5 anurans; Creusere and Whitford, 1976; Heatwole, 1982). A more complete picture of climatic conditions in the Florida Miocene must await the analysis of additional fossil faunas from other appropriately aged localities.

Equitability. Equitability is an assessment of the dominance or lack of dominance, in terms of numbers of individuals, of species within a community. It has traditionally been thought (MacArthur, 1965) that high equitability is a characteristic of stable environments, in particular those in the tropics. Recent studies on tropical anuran communities have shown that this assumption is erroneous; many tropical communities are dominated by one species

whose abundance is twice that of the next most abundant species (Scott, 1976; Heatwole, 1982). Little analysis of equitability in temperate anuran communities has been undertaken. The relative numbers of individuals of taxa found at the Thomas Farm locality are similar to those from forest habitats in North Carolina (Bennett et al., 1980). Both are characterized by a large number of bufonids. Narrow-mouth toads were abundant in the North Carolina study site, while at the Thomas Farm locality the next most numerous species (Hyla gratiosa) was present in less than half the abundance of Bufo. Equitability is somewhat greater at the Thomas Farm locality.

Resource partitioning and habitat preference. The analysis of community structure is concluded by assessment of the ways in which the Thomas Farm anurans may have divided their utilization of the habitat and its resources. Figure 6-15 shows the size range of anurans found at the locality. The largest frog was the rare Rana miocenica, which was approximately 74 mm in length. There is a high degree of size overlap of the frogs represented.

An assemblage of potentially competing taxa tends to partition resources as means of reducing competitive interactions (Pianka, 1966). Toft (1985), in her review of resource partitioning in reptiles and amphibians, concluded that resource partitioning could be divided into three major categories: habitat, food, and time. By scoring the relative importance of each category in the papers reviewed, she showed that habitat partitioning is most critical for post-metamorphic anurans. It is likely that such was the case at the Thomas Farm locality, as size ranges of frogs are not sufficently different to indicate that the animals were separating along a food resource continuum.

Habitat may be separated into two components; megahabitat and microhabitat (Toft, 1985). Examination of the habitat spectra and preferences of recent relatives of Thomas Farm anurans (Table 6-4) indicates that the Thomas Farm frogs were probably partitioning megahabitat. Bufonids, pelobatids, and microhylids are considered leaf-litter species, spending most of their time on the ground. Pelobatids and microhylids also may construct shallow burrows. Leaf litter species at Thomas Farm are dominated by Bufo praevius which accounts for 57% of the number of individuals in the anuran fauna. Aquatic or pond-margin species spend most of their time in or around semi-permanent to permanent bodies of water. Rana abava, Rana miocenica, Acris barbouri, and perhaps also Proacris mintoni frequented this megahabitat. Members of the genus Hyla usually live on terrestrial vegetation. The amount of partitioning of this part of the habitat depends on the structural diversity of the vegetation. The presence of one type of hylid in greater numbers than any of the others may indicate that there was not a high degree of vegetational diversity.

The presence of large numbers of frogs with similar size ranges and similar transformation sizes (Table 6-5) leads to speculation that anuran larvae were also competing for resources. Breeding sites may be partitioned (Heyer et al., 1975; Toft, 1985) in several ways. The most common is the selection by adults of temporary versus permanent breeding sites. A number of the frogs at Thomas Farm probably bred in transient water sources not directly associated with the locality (see previous discussion), while those that bred in more permanent water sources are common in the lower aquatic layers. It is

also possible that breeding times were separated temporally. In this way, many species may use a water source, but breeding times are staggered so as to minimize overlap (Wiest, 1982; Crump, 1982).

Final conclusions concerning the anuran community at Thomas Farm may be drawn by comparision of the fauna with that in recent communities (Table 6-5). All the fossil anuran genera, and even some of the species, are the same as those found in Florida today. The species represented may be found in xeric areas such as sandhill pine scrub assemblages, or more mesic forests (Bennett et al., 1980, Campbell and Christman, 1982). The relative rarity of Scaphiopus may indicate that soil type in the region was not suited for burrowing. The rarity of pelobatids at the site is somewhat unusual, as many Pleistocene cave and sinkhole deposits in Florida are characterized by overwhelming numbers of this frog. The presence of hylids indicates that tall vegetation was probably present. Unfortunately the type of vegetation present will never be known, as pollen was not preserved at the site (M. Binford, pers. comm.). The lack of large ranids was discussed by Holman (1967), who noted that their absence may have been the result of a lack of deep, permanent water in the region. The sizes of the frogs present, and the transformation times of recent relatives supports this conclusion (Table 6-5). The above analysis presents a picture of an anuran fauna that was essentially modern in composition and probably very similar to anuran assemblages found in the southeast today.

Community Analysis of the Thomas Farm Urodela

Only three species of urodeles, each representing a different family, are known from the Thomas Farm locality. The most common

species is the salamandrid Notopthalamus robustus (Estes, 1963). The highest numbers of individuals of N. robustus are found in the lower, presumably more aquatic layers of the site (Chapter 5). Recent members of the genus occur in Florida today, and are totally aquatic, although in more temperate regions the eft stage is terrestrial (Estes, 1963; Conant, 1975). It cannot be determined from examination of the fossil material if the eft stage was terrestrial or aquatic (Estes, 1963).

Siren hesterna was described by Goin and Auffenberg (1955) on the basis of one vertebra. Estes (1963) described the morphology of a second vertebra of this taxon. Since that time, only a few more elements, primarily vertebrae, of Siren hesterna have been collected. Today, the genus Siren is characterized by forms that live in stagnant, quiet waters (Estes, 1963; Conant, 1975). The rarity of this animal at the Thomas Farm locality may mean that suitable conditions for its survival were not available in the immediate area.

The third urodele present at the Thomas Farm, Batrachosauroides dissimulans, was first described from a fossil locality in Texas (Taylor and Hesse, 1943). The original description was based on a skull. Auffenberg (1958) referred several vertebrae to this species and erected a new family, the Batracosauriodidae. Estes reported the presence of B. dissimulans from Thomas Farm based on an atlas. Like Siren, B. dissimulans is relatively rare. As the family is totally extinct, little can be said concerning its mode of life or habitat, although according to Taylor and Hesse (1943), and Estes (1963), the skull possesses a number of neotenic features characteristic of aquatic salamanders.

Reptilia

Chelonia

Three species of turtle are known from the Thomas Farm. The most common species is the tortoise Geochelone tedwhitei (Williams, 1953). This animal evidently attained large size, but no complete or even partial shells have been recovered. The majority of elements found of G. tedwhitei are isolated pleurals and plastron fragments. Recent members of the genus are today confined to tropical regions as they do not burrow or hibernate and thus have no way of escaping cold weather (Hibbard, 1960). It is thus unlikely that G. tedwhitei was able to withstand prolonged periods of freezing temperatures, and its presence at the site indicates that the climate in the Miocene of Florida was probably more equable than the weather in this region today.

The emydid Pseudemys has also been reported from the Thomas Farm locality (Williams, 1953; Rose and Weaver, 1966), although remains of this turtle are fairly uncommon. The most recently uncovered sediments appear to have a higher proportion of Pseudemys elements than do the upper layers, indicating that standing water may have been present in the lower levels. Recent species of Pseudemys, in particular Pseudemys scripta inhabit quiet, vegetated ponds or sinkholes. They frequent habitats where water depth is no more than a few feet. At certain times of the year, Pseudemys are known to migrate over dry land (Ashton and Ashton, 1985).

Another species of emydid, the chicken turtle Deirochelys, was described by Jackson (1978). This turtle is rare at the site, and few specimens are known. Two species of Deirochelys are known in Florida today, and both inhabit quiet, shallow bodies of water (Ashton and

Ashton, 1985). The absence of other aquatic turtles such as softshell turtles or snappers may indicate that the water source at the locality was not permanent (Williams, 1953), or was very shallow. The absence of these two groups of piscivorous turtles may also be related to the near absence of fish from the locality.

Crocodylia

The alligator Alligator olseni was described by White (1942b), on the basis of a nearly complete skull and unassociated lower jaw. Much of the alligator material recovered from the site consists of osteoderms. The majority of remains are from small individuals; alligators of large size are rare at the site. The presence of alligators indicates that a suitable habitat, if not at the locality itself, was present nearby. The presence of these reptiles provides evidence that the climate was no cooler than southern regions where alligators are found today.

Lacertilia

The lizard fauna from Thomas Farm was described by Estes in 1963. On the basis of material then available, he described four genera of iguanids, Leiocephalus sp. and three undetermined genera, an undetermined genus of gekko, the skink Eumeces sp., the teid Cnemidophorus, an unidentified anguid, and tentatively the gila monster Heloderma. The identification of Peltosaurus from the Thomas Farm (Vanzolini, 1952), was rejected by Estes on the basis of the difference in preservation of the described specimen compared to other Thomas Farm elements. My recent screenwashing and matrix picking efforts have resulted in the recovery of osteoderms that belong to an animal closely related to Peltosaurus (P. Meylan, pers. comm).

Several of the species of lizards from Thomas Farm have tropical distributions today. The genus Leiocephalus is West Indian, and gekkos are also tropical in their distribution. Of seven species of gekkonid present in Florida today, only one, the reef gekko of the Florida Keys, is native (Ashton and Ashton, 1985). As Estes (1963) pointed out, little information relevant to Miocene habitat or climate in Florida can be obtained by a study of the lizard fauna as it is currently known. The majority of the families and genera known are found in a wide variety of geographical regions and habitats today. The information presently available allows only a general comparision of the lizard fauna of the Thomas Farm with the modern lizard fauna of Florida. The presence of large numbers of skinks, based on MNI from unit 15 (Table 6-6) may mean that soil conditions were sandy, as many species of present-day skink burrow in sand (Ashton and Ashton, 1985). Many recent teids and some iguanids are semi-arboreal (Ashton and Ashton, 1985). The presence of large numbers of individuals of these families could indicate that the habitat surrounding the locality was wooded. The presence of the gila monster could be taken as an indication that the region was a desert, however fossil evidence indicates that the family Helodermatidae was once widely distributed, and the present day distibution is evidently relictual (Pregill, pers. comm).

Serpentes

The fossil snake fauna of Thomas Farm is significant because it records one of the last known appearance of boids and the first known appearance of colubrids in North America (Auffenberg, 1963a). This locality was evidently sampling the period in which the early,

primitive boids were being replaced by the advanced colubrids. Three species of boid are known from the Thomas Farm locality. The most common form was described by Vanzolini (1952) as two species of Neurodromicus: N. stanolseni, and N. barbouri. Auffenberg (1963a) reassigned both species to the new genus and species Pseudoepicrates stanolseni. He speculated that these forms were probably both arboreal and terrestrial, much like their present day relatives. The two other species of boid, Ogmophis pauperrimus (Vanzolini, 1952), and Calamagras floridanus (Auffenberg, 1963a), were both described by Auffenberg as semifossorial forms that may have burrowed in leaf litter or loose sand. Two species of small colubrid were also described by Auffenberg (1963a); Pseudocemophora antiqua, and Paraoxybelis floridanus. The family Aniliidae is represented by the small fossorial Anilioides minuatus. Recent matrix picking has resulted in the recovery of a small, as yet unidentified snake of the family Typhlopidae. Members of this family are highly fossorial (P. Meylan, pers. comm).

To date, relatively little paleoecological analysis of the reptiles, in particular the lizards and snakes, can be undertaken. The large amount of new material consisting of better specimens of previously described taxa as well as some new taxa must be examined and identified before a thorough analysis can be made.

Figure 6-1. Least-squares regression of height of acetabulum of ilium on snout-vent length for recent bufonids. The equation for this line is: height of acetabulum = 0.524 (snout-vent length) + 0.007. Number of specimens = 22, R^2 = 0.97

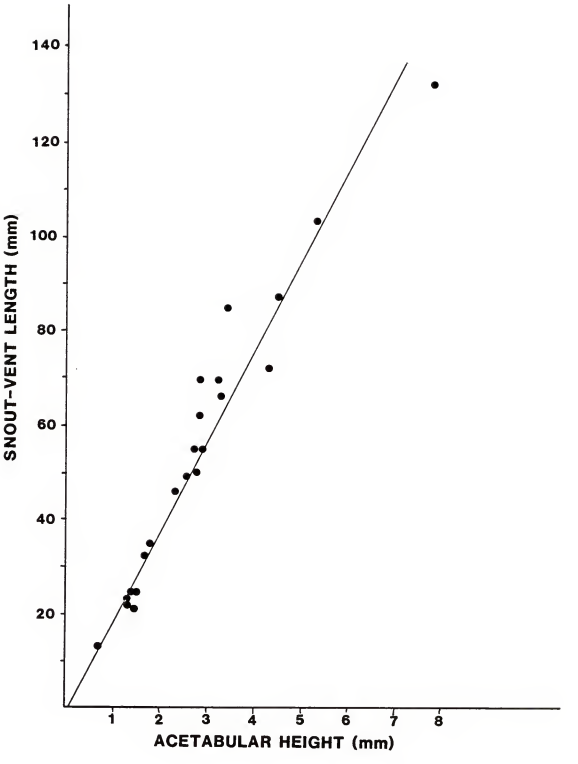

SNOUT-VENT LENGTH (mm)
140
120
100
80
60
40
20
1
2
3
4
5
6
7
8
ACETABULAR HEIGHT (mm)

Figure 6-2. Estimated size range of Bufo praevius compared with size ranges of Recent North American bufonids. Size data for modern species from Wright and Wright (1949).

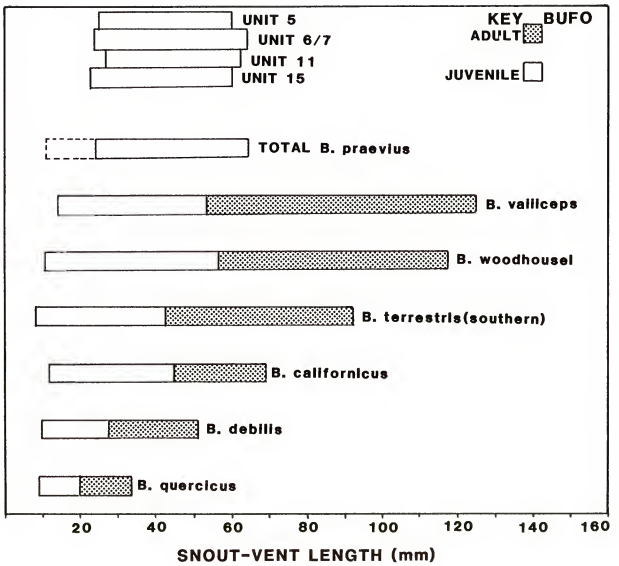

UNIT 5
UNIT 6/7
UNIT 11
UNIT 15
KEY BUFO
ADULT
JUVENILE
TOTAL B. praevius
B. vallicep
B. woodhousei
B. terrestris(southern)
B. californicus
B. debilis
B. quercicus
20
40
60
80
100
120
140
160
SNOUT-VENT LENGTH (mm)

Figure 6-3. Size-frequency histograms of acetabular heights of ilia of Bufo praevius from major sedimentary units at Thomas Farm.

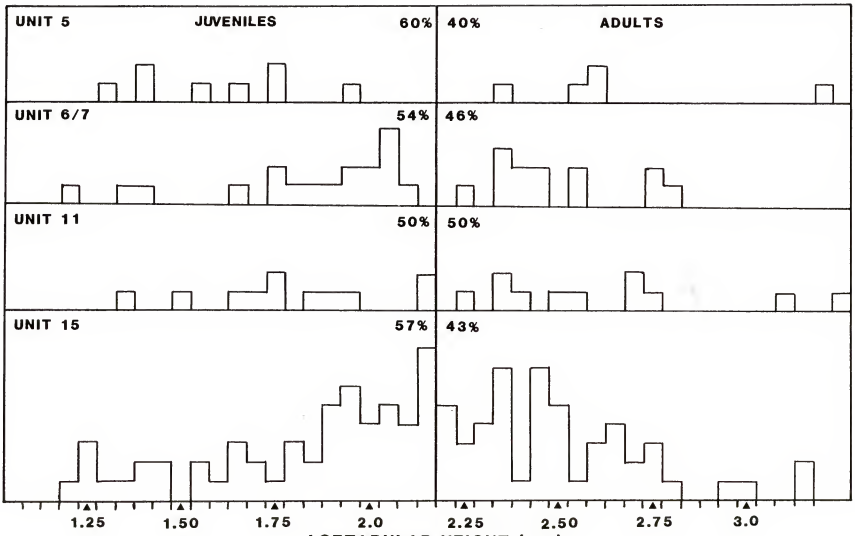

UNIT 5
JUVENILES
60%
40%
ADULTS
UNIT 6/7
54%
46%
UNIT 11
50%
50%
UNIT 15
57%
43%
1.25
1.50
1.75
2.0
2.25
2.50
2.75
3.0
ACETABULAR HEIGHT (mm)

Figure 6-4. Frequency-size histograms of populations of fossil Bufo praevius from Thomas Farm, samples from all units combined.

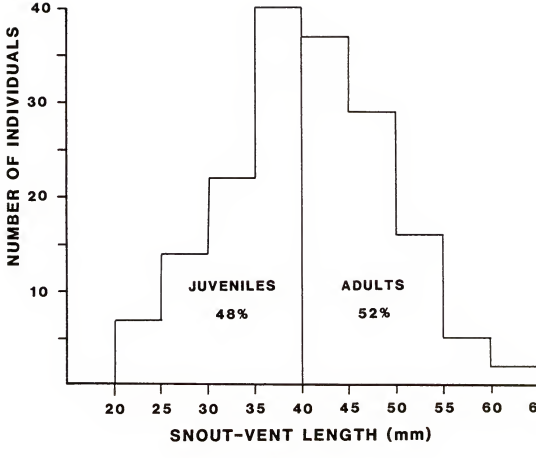

NUMBER OF INDIVIDUALS
40
30
20
10
JUVENILES
48%
ADULTS
52%
20
25
30
35
40
45
50
55
60
65
SNOUT-VENT LENGTH (mm)

Figure 6-5. Survivorship (of cohort of 1000 individials) of Bufo hemiophrys (data from Kelleher and Tester, 1969).

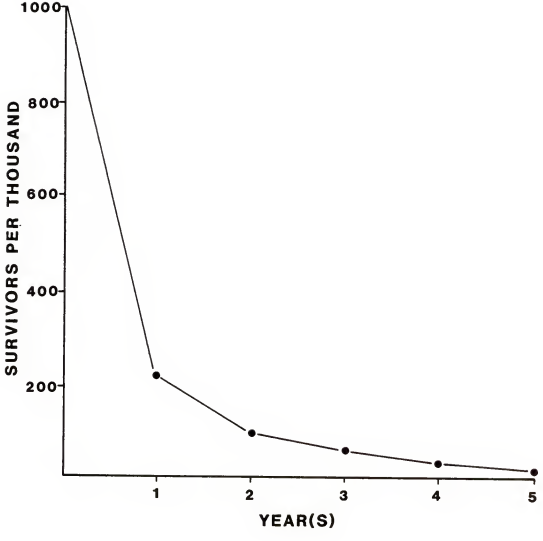

1000
800
600
400
200
SURVIVORS PER THOUSAND
1
2
3
4
5
YEAR(S)

Figure 6-6. Frequency size histogram of a breeding aggregation of Bufo terrestris (data from Raney and Lachner, 1947.

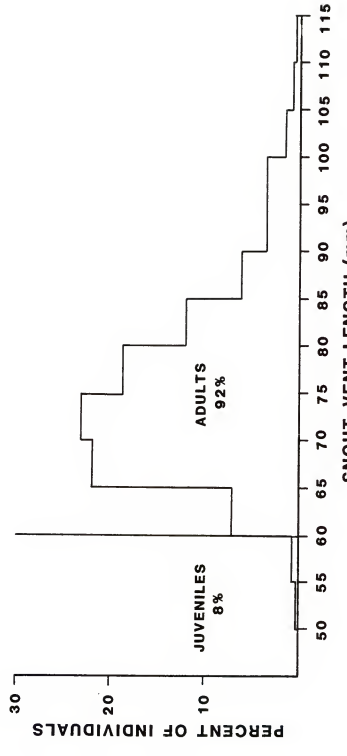

PERCENT OF INDIVIDUALS
30
20
10
JUVENILES
8%
ADULTS
92%
50
55
60
65
70
75
80
85
90
95
100
105
110
115
SNOUT-VENT LENGTH (mm)

Figure 6-7. Size ranges of fossil and Recent hylids. a) Hyla goini from Thomas Farm; b) Acris barbouri from Thomas Farm. Size range data for recent species from Wright and Wright, (1949), and Conant (1975).

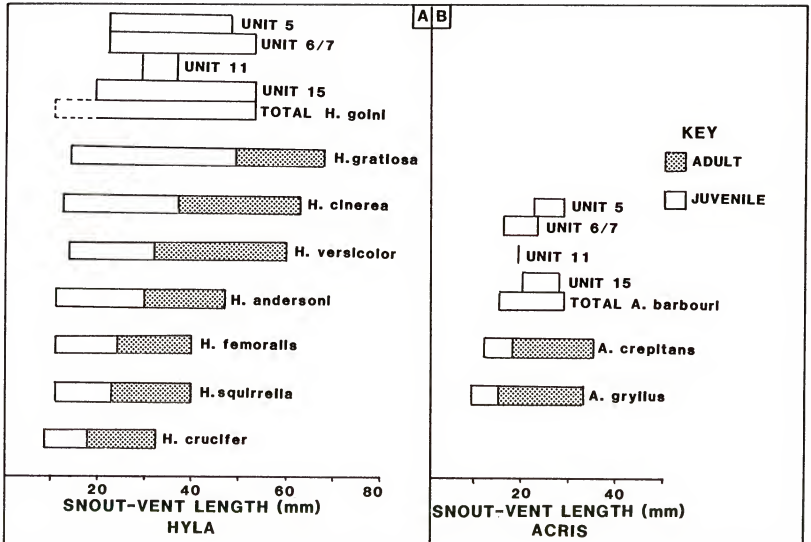

A
B
UNIT 5
UNIT 6/7
UNIT 11
UNIT 15
TOTAL H. goini
H.gratiosa
H. cinerea
H. versicolor
H. andersoni
H. femoralis
H.squirrella
H. crucifer
20
40
60
80
SNOUT-VENT LENGTH (mm)
HYLA
KEY
ADULT
JUVENILE
UNIT 5
UNIT 6/7
UNIT 11
UNIT 15
TOTAL A. barbouri
A. crepitans
A. gryllus
20
40
SNOUT-VENT LENGTH (mm)
ACRIS

Figure 6-8. Least-squares regression of height of acetabulum on snout-vent length for recent hylids. Equation for line is: height of acetabulum = 0.0382 (snout-vent length) + 0.222. Number of specimens = 28, R^2 = 0.95.

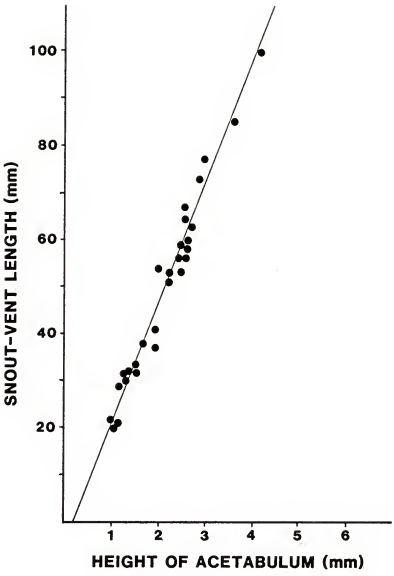

SNOUT-VENT LENGTH (mm)
100
80
60
40
20
1
2
3
4
5
6
HEIGHT OF ACETABULUM (mm)

Figure 6-9. Frequency-size histograms of acetabluar height of ilia of Hyla goini from major sedimentary units at Thomas Farm.

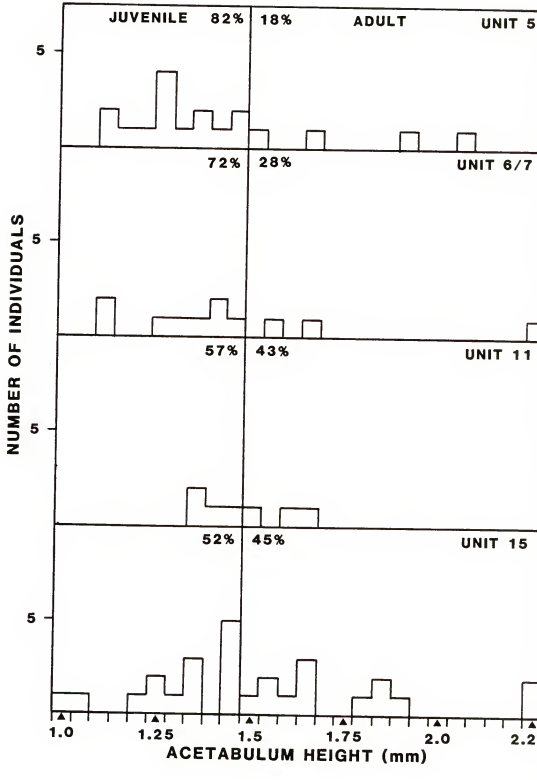

JUVENILE
82%
18%
ADULT
UNIT 5
72%
28%
UNIT 6/7
57%
43%
UNIT 11
52%
45%
UNIT 15
NUMBER OF INDIVIDUALS
5
5
5
5
1.0
1.25
1.5
1.75
2.0
2.25
ACETABULUM HEIGHT (mm)

Figure 6-10. Frequency-size histograms of acetabluar height of ilia of Acris barbouri from major sedimentary units at Thomas Farm.

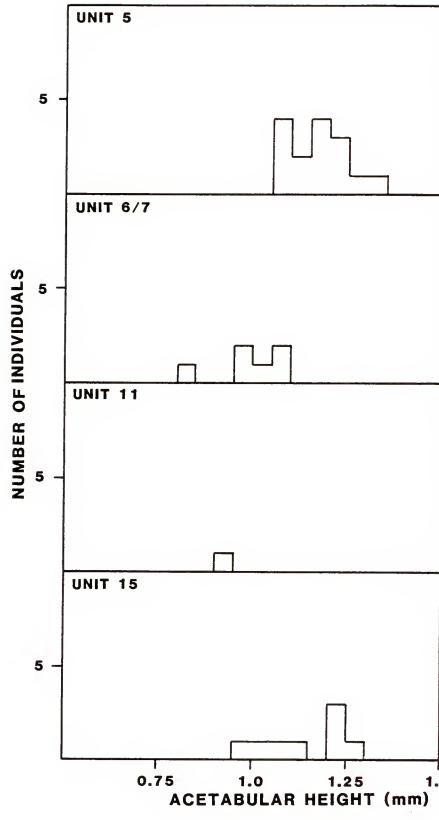

UNIT 5
5
UNIT 6/7
5
UNIT 11
5
UNIT 15
5
NUMBER OF INDIVIDUALS
0.75
1.0
1.25
1.5
ACETABULAR HEIGHT (mm)

Figure 6-11. Least-squares regression of height of acetabulum on snout-vent length for Recent ranids. Equation for line is: height of acetabulum = 0.425 (snout-vent length) + 0.405. Number of specimens = 18. R^2 =

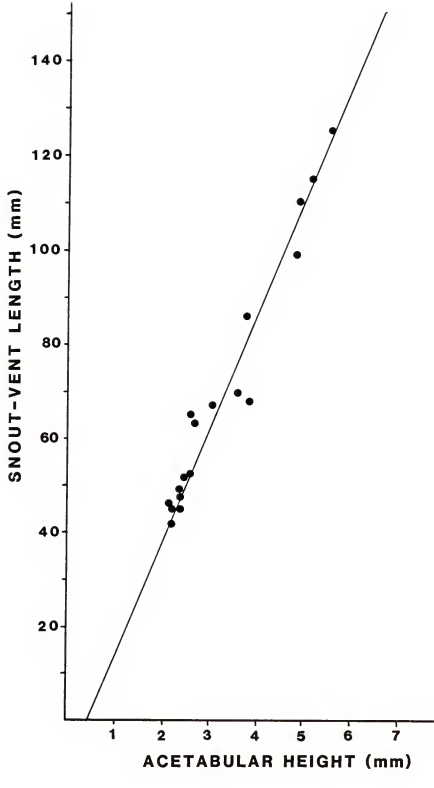

SNOUT-VENT LENGTH (mm)
140
120
100
80
60
40
20
1
2
3
4
5
6
7
8
ACETABULAR HEIGHT (mm)

Figure 6-12. Estimated size range of Rana abava from Thomas Farm compared to size ranges of Recent North American ranids. Size ranges of modern species from Wright and Wright (1949), and Conant (1975).

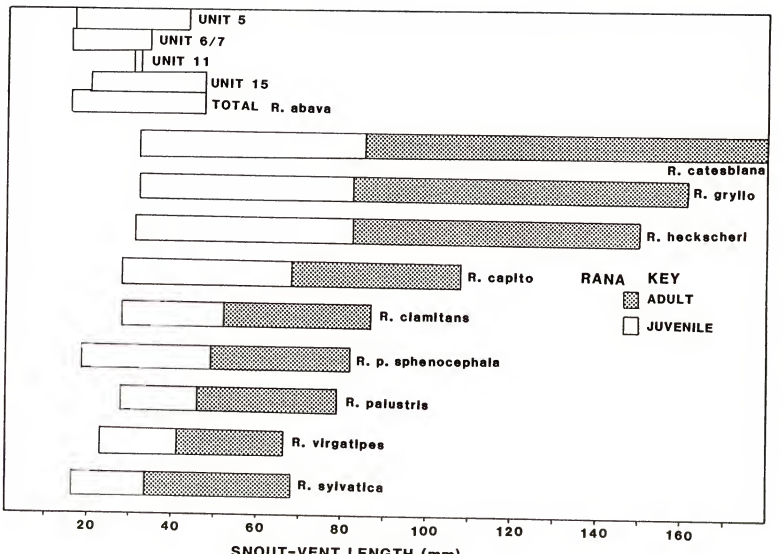

UNIT 5
UNIT 6/7
UNIT 11
UNIT 15
TOTAL R. abava
R. catesbiana
R. grylio
R. heckscheri
R. capito
R. clamitans
R. p. sphenocephala
R. palustris
R. virgatipes
R. sylvatica
RANA KEY
ADULT
JUVENILE
20
40
60
80
100
120
140
160
SNOUT-VENT LENGTH (mm)

Figure 6-13. Frequency-size histograms of acetabular height of ilia of Rana abava from major sedimentary units from Thomas Farm.

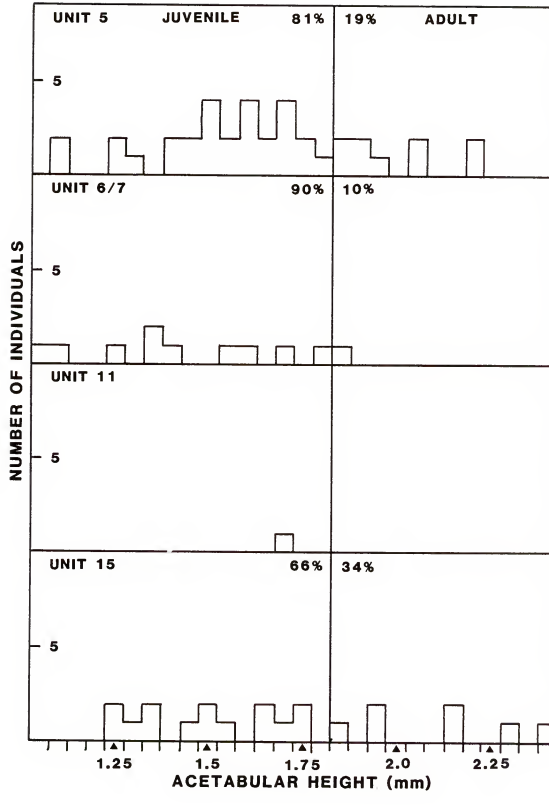

UNIT 5
JUVENILE
81%
19%
ADULT
5
UNIT 6/7
90%
10%
5
UNIT 11
5
UNIT 15
66%
34%
5
NUMBER OF INDIVIDUALS
1.25
1.5
1.75
2.0
2.25
ACETABULAR HEIGHT (mm)

Figure 6-14. Frequency-size histogram of predicted snout-vent length of Rana abava from unit 5.

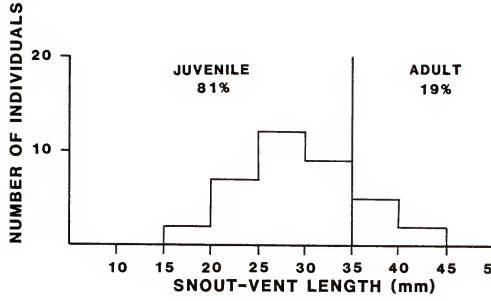

NUMBER OF INDIVIDUALS
20
10
JUVENILE
81%
ADULT
19%
10
15
20
25
30
35
40
45
50
SNOUT-VENT LENGTH (mm)

Figure 6-15 Size ranges of assemblages of fossil and modern frogs. a) Fossil anurans from Thomas Farm; b) Recent anurans from an oak-hickory forest in North Carolina (data from Bennett et al., 1980). Dashed lines indicate lack of specimens for portions of size range.

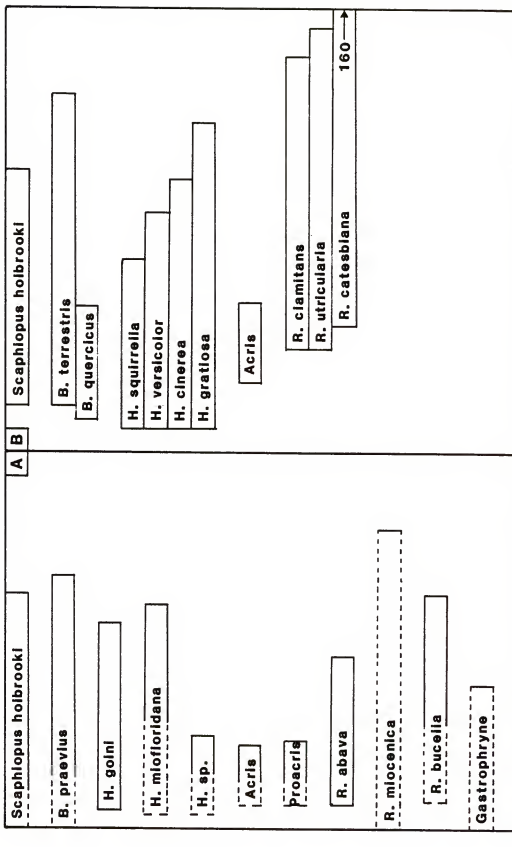

Scaphiopus holbrooki
B. praevius
H. goini
H. miofloridana
H. sp.
Acris
Proacris
R. abava
R. miocenica
R. bucella
Gastrophryne
A
B
Scaphiopus holbrooki
B. terrestris
B. quercicus
H. squirrella
H. versicolor
H. cinerea
H. gratiosa
Acris
R. clamitans
R. utricularia
R. catesbiana
160
10 20 30 40 50 60 70 80
10 20 30 40 50 60 70 80 90
SNOUT-VENT LENGTH (mm)

Table 6-1. Species of recent anurans examined in this study. Specimens obtained from UF Herpetology Collection.

Taxon	No. of specimens measured
Bufonidae	
Bufo alvarius	2
Bufo boreas	1
Bufo debilis	2
Bufo quercicus	5
Bufo terrestris	6
Bufo valliceps	3
Bufo woodhousei	3
Hylidae	
Acris gryllus	3
Hyla boans	1
Hyla cinerea	3
Hyla chrysoscelis	1
Hyla dominicensis	1
Hyla gratiosa	12
Hyla regilla	1
Hyla squirrella	5
Hyla vasta	1
Ranidae	
Rana aerolata	2
Rana grylio	6
Rana heckscheri	1
Rana palmipes	1
Rana pipiens	6
Rana utricularia	1
Rana virgatipes	4
Microhylidae	
Gastrophryne carolinensis	1

Table 6-2. Growth rates of Recent species of Bufo. Max. Length indicates largest known length of species. Trans. length is transformation length, or length of newly metamorphosed individuals. Total growth is obtained by subtracting transformation length from maximum length. Year 1 growth is the amount of length added to the transformation length at the end of the first season. % Tot. is the percentage of total growth attained by the end of the first season (or second season). Year 2 growth is the amount of total length added to the transformation length by the end of the first full year of life (end of second season).

Species	Max. Length	Trans. Length	Total Growth	Year 1 Growth	% Tot.	Year 2 Growth	% Tot.
Bufo quercicus[+]	30 mm	10 mm	20 mm	11 mm	55	19 mm	95
Bufo hemiophrys[*]	64 mm	11 mm	53 mm	11 mm	20	32 mm	59
Bufo terrestris[#]	115 mm	10 mm	105 mm	20 mm	19	60 mm	57
Bufo valliceps[©]	125 mm	10 mm	115 mm			70 mm	61

[+] Data from Turner, 1960.
[*] Data from Tester and Breckenridge, 1964.
[#] Data from Hamilton, 1934.
[©] Data from Blair, 1953.

Table 6-3. Age-size classes and growth rates of Recent species of Hyla*. Max. juv. size indicates maximum size of juveniles found. Juv. growth is amount of length added to transformation length. For explanation of other terms see Table 6-2.

Species	Maximum Length	Transform. Length	Total Growth	Max. Juv. Size	Juv. Growth	% of Tot.
H. crucifer	33 mm	9 mm	24 mm	18 mm	9 mm	38
H. squirrella	37 mm	11 mm	26 mm	23 mm	12 mm	46
H. femoralis	40 mm	10 mm	30 mm	24 mm	14 mm	46
H. andersoni	47 mm	11 mm	36 mm	30 mm	19 mm	52
H. versicolor	60 mm	13 mm	47 mm	32 mm	19 mm	40
H. cinerea	63 mm	12 mm	51 mm	37 mm	25 mm	49
H. gratiosa	68 mm	14 mm	54 mm	49 mm	35 mm	64
Means		11 mm				47

*Size range data from Wright and Wright, 1949.

Table 6-4. Relative abundances, in MNI per species, of anurans from Thomas Farm.

Taxon	UNIT 5 MNI	UNIT 5 Percent of Total	UNIT 6 MNI	UNIT 6 Percent of Total
Scaphiopus holbrooki	1	1.1	1	1.9
Bufo praevius	14	16.1	29	53.7
Hyla goini	18	20.7	9	16.6
Hyla miofloridana	0	0	0	0
Hyla new sp.	2	2.3	0	0
Proacris mintoni	1	1.1	0	0
Acris barbouri	14	16.1	6	11.1
Rana abava	32	36.8	7	12.9
Rana bucella	5	5.7	2	3.7
Rana miocenica	0	0	0	0
Gastrophryne sp.	0	0	0	0

Taxon	UNIT 11 MNI	UNIT 11 Percent of Total	UNIT 15 MNI	UNIT 15 Percent of Total
Scaphiopus holbrooki	0	0	1	0.6
Bufo praevius	28	66.6	123	73.7
Hyla goini	11	26.6	28	16.7
Hyla miofloridana	0	0	0	0
Hyla new sp.	0	0	1	0.6
Proacris mintoni	0	0	0	0
Acris barbouri	1	2.4	1	0.6
Rana abava	1	2.4	12	7.2
Rana bucella	0	0	0	0
Rana miocenica	0	0	0	0
Gastrophryne sp.	0	0	0	0

Taxon	ALL UNITS COMBINED MNI	ALL UNITS COMBINED Percent of Total
Scaphiopus holbrooki	3	0.9
Bufo praevius	194	55.6
Hyla goini	66	18.9
Hyla miofloridana	0	0
Hyla new sp.	3	0.9
Proacris mintoni	1	0.3
Acris barbouri	21	6.0
Rana abava	52	15.0
Rana bucella	7	2.0
Rana miocenica	0	0
Gastrophryne sp.	0	0

Table 6-5. Comparison of recent species of anurans with Thomas Farm anurans.

	Habitat	Breeding	Days to transform	Trans. Size(mm)
FOSSIL *Scaphiopus holbrooki*				
RECENT				
Same	Forest floor Shallow burrows	Mar./Sept. Temporary ponds	14-60	8.5-12
FOSSIL *Bufo praevius*				
RECENT				
Bufo terrestris	Pinelands, Ubiquitous	Mar./Aug. Temporary ponds	30-55	6.5-1
FOSSIL *Hyla goini*				
RECENT				
Hyla femoralis	Pinebarrens Trees	Apr./Sept. Bogs, Temp. ponds	50-75	13
FOSSIL *Acris barbouri*				
RECENT				
Acris crepitans	Creeks, Ponds Meadows	Feb./Oct. Permanent or temporary ponds	50-90	9-15
FOSSIL *Rana abava*				
RECENT				
Rana pipiens	Lake margins Ponds	Feb./Dec. Permanent ponds	20-70	20-33
FOSSIL *Gastrophryne cf. carolinensis*				
RECENT				
Same	Leaf litter under logs	May/Sept. Temporary ponds	20-70	8.5-1

Table 6-6. Families and MNI of Lizards from unit15, Thomas Farm. Weight of matrix sample = 190 kg.

Family	MNI	Family known in North Florida today
Anguidae	4	yes
Gekkonidae	2	introduced
Helodermatidae	1	no
Iguanidae	4	yes
Scincidae	12	yes
Teiidae	9	yes
Unident.	6	

CHAPTER 7
AVES, INSECTIVORA, AND CHIROPTERA

Several major groups of vertebrates from Thomas Farm are represented by large amounts of material, but the faunas are essentially undescribed. The birds and bats are the most notable of these groups. This chapter will discuss the information presently available on these two taxa. The Insectivora are represented by one species only, a small soricid that has been referred tentatively to Limnoecus (C. E. Ray, pers. comm.).

Aves

Several of the larger, non-passerine bird taxa from Thomas Farm have been described. Wetmore (1943) described Rhegminornis calobates, and assigned the genus to the Charadriiformes. He also noted the presence of a columbid (dove) and a warbler at the locality, based on fragmentary material. Brodkorb (1954) described a chachalaca, Boreotalis laesslei, a cormorant Phalacrocorax subvolans (1956), and a kite, Promilio (Proictinia) floridana (1956). Wetmore (1958) named two additional species of kite, P. epileus and P. brodkorbi. Olson and Farrand (1974) redescribed Rhegminornis calobates as an early Miocene turkey moving it to the Galliformes. Becker (in press) reassigned the specimens identified as Phalacrocorax to the Anhingidae.

Based on the known fauna, little can be inferred concerning the paleoecology or the habitat of the Thomas Farm birds. Chachalacas today have a tropical distribution (Brodkorb, 1954), and recent kites

are known from tropical and subtropical regions (May, 1935). The presence of these groups provide evidence that the climate was tropical to subtropical. Three species of kite are known in Florida today. Two of these species feed on small mammals, reptiles, anurans, and insects, and the third, the Everglades Kite, is a snail specialist (May, 1935). It is possible that the fossil raptors may have been in part responsible for the large microfaunal accumulation of unit 15 (see Chapter 4). The presence of an anhinga may be taken as an indication of an aquatic environment at the locality, however, specimens of this species are very rare. As these birds feed almost exclusively on fish, the lack of fish fossils at the site indicates that conditions were not suitable to support a population of anhingas.

The dearth of described specimens of birds from Thomas Farm does not mean that bird fossils from this locality are rare, in fact comparatively speaking, the Thomas Farm bird assemblage is among the richest in North America. The site is particularly important as it provides one of the earliest and best records of passerine birds in North America (S. Olson, pers. comm.). The majority of species have yet to be examined and described.

Chiroptera

Only two species of bat have been reported from the Thomas Farm. Lawrence (1943) described two new genera and species of vespertilionid, Suaptenos whitei and Miomyotis floridanus. She also tentatively referred 2 mandible fragments to Eptesicus. Since the publication of Lawrence's paper, screenwashing efforts have resulted in the recovery of a large number of fossil bat specimens, including complete dentaries and limb elements. According to G. Morgan, who

currently is studying the Thomas Farm bats, at least six species of bat are present at the site, and all belong to groups whose recent day members are insectivorous and are obligate cave dwellers. The largest number of chiropteran specimens per kilogram of matrix has been recovered from Unit 15, the microfaunal layer (see Chapter 4). The presence of large numbers cave-dwelling bats at the site, in particular in the upper unit 15 (see Chapter 4) indicates that the locality provided a suitable habitat (i.e., caves) for these animals. Morgan also notes the presence of two families of bat at the site that today have totally tropical distributions. A complete analysis of the bat fauna is underway, and results of this study will be forthcoming.

CHAPTER 8
RODENTIA

Rodents are the most abundant mammals at the Thomas Farm locality. The micromammalian fauna is dominated by the small heteromyid Proheteromys floridanus, described by Wood (1932, 1935, 1947) and Black (1963a). The larger and considerably more rare Proheteromys magnus is also known from the site (Wood, 1935, 1947; Black, 1963a). Other members of the rodent fauna include three species of sciurid, an extremely rare eomyid, and one tooth that Black (1963a) tentatively referred to the Cricetidae. This analysis will concentrate mainly on Proheteromys floridanus, as this species is represented by a large sample of cranial and postcranial material. The other species for which fewer specimens are available cannot be investigated as completely, although they will be discussed briefly.

Assessment of the habitat preferences and ecological requirements of an animal requires analysis of the organism's morphology and comparison of the animal with recent forms. Morphological characteristics of the teeth, such as crown height and development of lophs provide information concerning possible dietary preferences. Limb and body morphology and limb ratios indicate the main type of locomotion employed by the mammal.

Body size is also an important parameter in ecological analysis. Body mass has been shown to be related to population density (Damuth, 1981) life span, and metabolic rate (McNab, 1963, 1970, 1980; Martin, 1980). This chapter will deal with the following topics;

1. A discussion of the problems encountered in the determination of body sizes of fossil mammals, and estimates of the body sizes of the rodents from Thomas Farm.

2. Analysis of the cranial and postcranial morphology of Proheteromys floridanus and P. magnus as a means of determining possible diet, locomotion type, and preferred habitat.

The analysis of life history parameters will be discussed in the section on site paleoecology. Recent and fossil specimens used are discussed in Chapter 2.

The in-depth investigation of one fossil genus (Proheteromys) will hopefully serve to demonstrate that with careful analysis the basic morphology, habitat requirements, diet, means of locomotion, and ecological parameters of extinct species can be inferred with a high degree of confidence. A strong paleoecological interpretation of a fauna depends on many such studies of the animals involved. Heteromyid rodents were specifically chosen since analysis of this group will also be of use in the investigation of other as yet unstudied Florida Miocene sites that are dominated by this family of rodents.

Heteromyidae

The analysis of Proheteromys floridanus and P. magnus is most interesting because the rodents of the family Heteromyidae show a high degree of diversification in preferred habitat, morphology, and means of locomotion. Little is known about the postcranial morphology of many of the fossil heteromyids. The family is divided into three subfamilies based primarily on characteristics of the cheekteeth (Wood, 1935; Lindsay, 1972). The Heteromyinae are traditionally considered the most primitive members of the family. The two living

genera, Liomys and Heteromys, are both scansorial and essentially quadrupedal (Eisenberg, 1963; Pinkham, 1973), although a fossil heteromyine, Diprionomys agrarius, was shown by Wood (1935) to have saltatorial characteristics. Liomys inhabits seasonally dry to fairly arid regions (Fleming, 1971, Fleming and Brown, 1975). Members of the genus Heteromys are found in tropical forests having high seasonal rainfall (Rood and Test, 1968; Fleming and Brown, 1975). Members of both genera have rooted, high crowned teeth.

The Perognathinae is a large subfamily with numerous fossil and modern forms. Recent members of the group belong to the genera Perognathus and Microdipodops. Perognathines range from scansorial to richochetal in locomotion, and their teeth show varying degrees of hypsodonty. Many of the recent species of Perognathus possess cuspidate, low-crowned teeth and are quadrupedal and scansorial (Bartholomew and Carey, 1954; Pinkham, 1973). Pocket mice live in a variety of habitats ranging from mesic scrub to xeric prairie and desert (Blair, 1937; Arnold, 1942; Reynolds and Haskell, 1949; Alcoze and Zimmerman, 1973; Van de Graaf, 1973). The Dipodomyinae are characterized by extreme modification of teeth and postcrania (Wood, 1935; Howell, 1932). Their morphology reflects the adaptations to the desert environments in which they live. The teeth of recent dipodomyines are very high-crowned and almost rootless, with enamel restricted to the anterior and posterior regions of the cheekteeth. The cheektooth crown pattern is lost early in life, and teeth are compressed in the anterior-posterior plane. All recent members of the subfamily belong to the genus Dipodomys and are adapted for saltatory locomotion, possessing elongate hind limbs (Howell, 1932; Wood, 1935).

Proheteromys floridanus and P. magnus, as the generic name implies, are considered possible ancestors of the subfamily Heteromyinae (Wood, 1932; 1935), based primarily on the cusp pattern of the upper premolars. In heteromyines, the protoloph unites lingually with the metaloph on the upper premolar. However, in some recent perognathines this characteristic is also seen, particularly on worn teeth. The lower premolars of Proheteromys floridanus from Thomas Farm are actually more similar to those of perognathines than to heteromyines in the manner in which the lophs unite (Wood, 1935; Hall, 1981). The Heteromyidae is in need of systematic revision, the last major treatment of the group (Wood 1935) being somewhat out of date. It is beyond the scope of this study to undertake the revision, nor is it necessary at this point. The intent of this study is not to clarify the systematic standing of the genus Proheteromys, but to assess the ecology of the genus.

Body Size

Mammalian body size has been shown to be correlated with a number of cranial and postcranial measurements. Gingerich, Smith and Rosenberg (1982) showed that primate body mass was correlated with M_1 area, and Creighton (1980) plotted M_1 area against head and body length (total length minus tail length--see Hall, 1981) for a variety of mammals. Martin (1980, 1984) demonstrated that body mass in cricetines is proportional to the length of the M_1. Mammalian body mass may also be correlated with condylar width of the skull (Wing and Brown, 1979; Martin, 1980).

Postcranial measurements such as the width of the head of the femur have also been used as a means of predicting mammalian body mass

(Wing and Brown. 1979; Martin, 1980). In a number of the these studies, regression equations were constructed using measurements for many species of mammals. The majority of these equations will not provide accurate body mass or body size estimates for very small mammals such as rodents, and a miscalculation of a few grams for an animal this size can be a significant error.

In studies that deal with mammals from selected orders, the accuracy of predictive regression equations is improved. However, within the Rodentia, morphological variation is extensive, and must be addressed if a regression of a chosen parameter with body size is to be constructed. For example, Creighton (1980) showed that body length can be correlated with area of the M_1 in rodents; however, within a given size range, rodents that retain the fourth premolar (sciurids, castorids, geomyids, heteromyids, hystricognaths, and zapodids) possess relatively smaller M_1s than do rodents that have lost the premolars (muroids).

Postcranial measurements may be subject to variation that is a function of locomotion type rather than allometry. Bipedal forms that possess elongate hind limbs often have larger femora (and hence larger femur heads) than do quadrupedal forms of similar body length. For the Rodentia, the majority of which are scansorial and quadrupedal, higher accuracy would be achieved by eliminating bipedal forms from the regression of hind limb measurements against body weight or length. A separate curve could be constructed for bipedal forms if desired.

Before discussing the various methods that can be used to determine body size of a fossil heteromyid, it is first necessary to

define the term "body size". To most workers, body mass is the best indicator of body size (Martin, 1980; Gingerich et al., 1982), but Creighton (1980) and Radinsky (1978), discussed the use of head and body length as an indicator of body size. As the latter measurement is a standard measurement taken by mammalogists, it is recorded for most specimens in mammalogy collections. Relatively few specimens possess weight data, particularly if the animal has been prepared as a skeleton. By using head and body length, it is possible, even with a mammal collection of small size, to obtain enough body size data on most rodent groups to perform regression analyses. For this reason, use of this measurement is justifiable. However, there have been no attempts to correlate head and body lengths with metabolic rates or estimates of population density, two parameters that are often used in paleoecological studies.

The most obvious solution to this problem is the construction of a regression curve relating rodent head and body length to body mass. Such a curve was constructed for quadrupedal rodents (primarily heteromyids), using data obtained on tags of 50 recent specimens from USNM and FSM mammalogy collections (Table 8-1, Figure 8-1). The two variables are very highly correlated with each other ($R^2 = 0.94$). The relationship of head and body length to mass has previously been demonstrated for carnivores and ungulates by Radinsky (1978). Although bipedal rodents were not included in the calculation of Figure 8-1, their measurements are plotted on the figure as a means of illustrating how their inclusion would decrease the accuracy of the regression. All saltatory forms considered, with the exception of the minute dipodid Salpingotus, possess greater body masses than expected

based on their head and body lengths. Body mass is greater for bipedal rodents than for quadrupedal rodents of similar head and body lengths due to the increase in mass of the hindlimbs of the former. In addition, fusion of vertebrae and slight shortening of the vertebral column of bipedal forms serve to reduce head and body length slightly as well (Hatt, 1932; Howell, 1932). In the following discussion of body size of fossil rodents, head and body length and body mass will both be considered. As it will be shown in the latter portion of this chapter that Proheteromys was a quadrupedal, scansorial form, this assumption is made somewhat prematurely in this section dealing with the calculation of body size.

Area of M_1. Area of the M_1 has been cited as an indicator of body mass and head and body length (Gingerich et al., 1982; Creighton, 1980). Table 8-1 lists (equations #2 and #3) and Figure 8-2 illustrates graphically, the regressions of M_1 area against body mass and head and body length, respectively, for recent scansorial heteromyids in the Florida State Museum Mammalogy collection. The R^2 values are 0.65 and 0.62 respectively. If data for Dipodomys is added, R^2 drops to .60 for body mass, and to .22 for head and body length. The calculated size of Proheteromys floridanus, based on the average M_1 area determined from 11 M_1s (Table 8-3) is 62.8 mm. The body weight based on M_1 area is 6.5 gm. Figure 8-1, which shows the relationship of head and body length to body mass, indicates that a 63 mm rodent would weigh about 7.2 gm, and that a 6.5 gm rodent would have a head and body length of 60.9 mm.

The average M_1 area of Proheteromys magnus is 2.57 mm (Table 8-3). This measurement is outside the ranges of the regression lines,

but if each line were extended, the predicted body mass of P. magnus is 3196 gm (over 6 pounds), and the predicted head and body length 359 mm. According to the regression in Figure 8-1, the head and body length of a 3196 gm rodent is approximately 423 mm, and the weight of a 359 mm rodent averages 3188 gm. These figures are excessively large, particularly when they are compared with the predicted body size values obtained from postcranial measurements of P. magnus (see below, and Figure 8-6). The large size estimate based on the M_1 area of P. magnus may reflect a trend seen in recent large heteromyids toward reduction in cheektooth size relative to body size. This trend may be related to the increase in size of the bulla and the concurrent reduction in the length of the toothrow. The regressions of recent sciurid M_1 areas against head and body lengths and body mass (Figure 8-8) provide more reasonable estimates of body size for P. magnus, 67 gm mass, and 133 mm body length. If Creighton's (1980) graph that relates rodent head and body length to M_1 area is used, predicted lengths of P. floridanus and P. magnus are 83 mm and 134 mm, respectively. These values are estimated from the regression line on p. 440 in his paper, as he did not list equations for any of the lines. The predicted length of P. floridanus using Creighton's regression is higher than those obtained in this study. The length estimate of P. magnus is far less than the value obtained in this study using the M_1 area measurement for heteromyids, but very similar to that calculated using the regression in Figure 8-8 and Table 8-9 for body mass and head and body length of sciurids.

Condylar width is a very reliable indicator of body mass (Radinsky, 1978; Wing and Brown, 1979; Martin, 1980), but this portion

of a small rodent skull is seldom fossilized. No posterior skull regions of Proheteromys floridanus or P. magnus are known. Postcranial elements are more reliable indicators of body size than are teeth (Wing and Brown, 1979, Martin, 1980). The measurement of the breadth of the heads of the humerus, femur, and tibia may all be used in determination of body size. The proximal articular regions of the limb bones appear to exhibit less morphological variation than do the distal ends.

Humerus. Table 8-1 lists the regression equations for the width of the humeral head against both body mass and against head and body length of recent quadrupedal heteromyids (Figure 8-3). The body mass regression has few points in the smaller size ranges (Table 8-2) with the result that the y-intercept of this equation is greater than the average size of the humeral head of Proheteromys floridanus. The predicted head and body length of P. floridanus is 63.9 mm, based on the average width of 50 humeral heads (Table 8-3). The size range of the species, based on the range in size of the proximal humeri, is shown in Figure 8-6, as is the predicted body weight range, determined indirectly from the head and body length (Figure 8-1). The one humerus specimen of P. magnus (see Table 8-3) provides a body weight estimate of 100 gm, and a head and body length prediction of 137 mm. According to the regression equation shown in Figure 8-1, a 100 gm quadrupedal rodent would have a head and body length of about 143 mm, and a 137 mm rodent would weigh about 87 gm. These values are closer to a more reasonable size estimate of P. magnus than those predicted on the basis of lower molar area. The head and body length estimate is also close to that obtained using Creighton's (1980) graph.

Femur. The size of the head of the femur of scansorial rodents is highly correlated with both head and body length, and with body mass (Table 8-1, Table 8-2, and Figure 8-4). The size of the femur head of P. floridanus is too small to permit an estimate of body weight directly from the body mass/femur head width regression, but the head and body length calculated from femur head width is 71.4 mm based on the average size of 100 fossil femur heads (Table 8-3). The corresponding body mass estimate based on body length is 10.7 gm. The size range of P. floridanus based on the range of femur head widths is shown in Figure 8-6. The predicted size of P. magnus, based on the measurement of one femur head is 87 gm in weight (correlated with a head and body length of 137 mm), and 135 mm in head and body length (correlated with a body mass of close to 85 gm). These mass and body length estimates are very similar to those obtained using the regression equations for body size against humeral head width. If Martin's (1980) equation for body mass based on femur head width is used, the predicted mass of Proheteromys floridanus is 27.7g, and the predicted body mass of P. magnus is 99.5 gm. The predicted values based on the regression equations presented by Wing and Brown (1979) are 31.9 gm for P. floridanus, and 100.6 gm for P. magnus. Both estimates of the weight of P. floridanus are considerably higher than the estimates obtained in this study, and are probably less accurate. The predicted weights for P. magnus, although high, are within 10 gm of some of the mass estimates in this study.

Tibia. The width of the proximal end of the tibia may be used to determine body size. Head and body length is more highly correlated with tibial width than is body mass (R^2 = .86 as opposed to .77;

Figure 8-5 and Table 8-1). The proximal end of the tibia of P. floridanus cannot be used to determine body mass using the regression equation in Table 8-1, as the measurement is smaller than the y-intercept of the regression equation. The predicted head and body length based on the average width of 50 proximal tibiae (see Table 8-3) is 72.8 mm, and the body mass of a quadrupedal rodent with a head and body length of 73 mm 11.4 g, based on equation #1 in Table 8-1. No tibiae of P. magnus are known.

Figure 8-6 shows the ranges and mean values of body weight and head and body length for Proheteromys floridanus and P. magnus. A wide size and weight range indicates that a large number of specimens were measured, and that a large portion of the population size, from juvenile to large adult, is represented. For the most part, the average size values calculated in this study of Proheteromys floridanus are very similar, indicating that the estimated values actually reflect the size of the living form. The size estimates of P. magnus are less reliable, due to the smaller sample sizes. The body mass measurements will be employed in the the chapter dealing with population ecology.

Morphology

Basic features of a mammal's life history such as diet and mode of locomotion can be determined to some extent by the investigation of its skeletal morphology. By comparing a fossil animal's morphology with that of a living form, it is possible to speculate on the possible habitat requirements of the fossil species. Diet of an extinct animal is most frequently inferred by examining cranial characteristics, particularly those of the teeth. The rodent dental

battery consists of a pair of ever-growing incisors that are separated from the cheekteeth by a large diastema. The number of cheekteeth varies from five to two; a number of early extinct groups and some species of living sciurids possess two premolars in addition to three molars, several families (including heteromyids) possess a fourth premolar, and muroids and several other groups have lost the premolars. The variety in cheektooth morphology is extensive, and many diverse groups have independently obtained similar cheektooth features. Although there is great diversity in tooth morphology, the fact remains that most rodents are primarily herbivorous, and animals with very different cheektooth morphology may in fact exhibit very similar dietary preferences.

Incisors. Rodents possess one pair of very specialized ever-growing incisors, although within the order there appears to be only minor variation in incisor morphology. Several features of incisors may be examined and a number of measurements taken to determine if the morphology of the incisor is related to type of food consumed.

Physical features that cannot be analyzed quantitatively include the outline shape of the occlusal end of the incisor, and the presence of grooves or ridges on the outer enamel band. The shape may be seen either by making a cross section through the tooth, or by examination of the occlusal surface. While it is almost impossible to relate the shape to preferred diet, the outline shape may be used to identify the incisor to taxon. It is possible to identify the incisor to genus (Wolff, 1973), and sometimes to species. Fossil rodent incisors used in this study were identified in this manner.

Grooves in the outer enamel band on the upper incisors are characteristic of several groups of rodents, including some members of the Heteromyidae. The functional significance of grooving, if any, is unknown. Merriam (1895) proposed that the grooves aid in holding the food in place while it is being cut by the lower incisors, and Wood (1935) suggested that the grooves increase the surface area of the enamel portion. While this feature is seen on the incisors of several groups of seed-eating rodents, it is also characteristic of rodents (such as pocket gophers) that feed on coarse vegetation. The fossil heteromyids Proheteromys floridanus and P. magnus have smooth incisors, as do modern heteromyines. Most perognathines and all dipodomyines possess grooved upper incisors.

There are a limited number of measurements that may be taken on rodent incisors, particularly if Recent specimens are used. In a modern specimen, only a small portion of the upper incisor can be seen, unless the tooth is removed from its alveolus. The two measurements taken on specimens used in this study were the transverse width of the enamel band, and the antero-posterior length of the incisor (or thickness), taken at the same level as the first measurement (Figure 2-6).

The measurements themselves have little meaning, as a large rodent will typically have larger incisors than a small rodent. In order to analyze the measurements, it is necessary to correct for the size differences of the rodents studied. For this reason, the two incisor measurements discussed above were treated as ratios to head and body length. This procedure serves to identify those features

that are primarily size dependent, as opposed to those that may be related to dietary preferences (Table 8-4).

Transverse widths of incisors to head and body lengths are listed in Table 8-4. Sciurid incisors (except those of Marmota) possess the smallest enamel band width relative to head and body length (0.0066-0.0088). A large number of families, including the Heteromyidae, have ratios of incisor transverse width to head and body length ranging from about 0.0090-0.010. Estimated ratios for Proheteromys floridanus based on mean incisor width (Table 8-3) divided by mean head and body length (Figure 8-7) are slightly higher at 0.011, while those for P. magnus are somewhat lower (0.0077). Geomyids, castorids, and Ctenomys possess the highest incisor width to head and body length ratios of all species measured, indicating that rodents that feed on coarse vegetation or use their teeth for burrow construction have relatively wider incisors than do those that feed on less resistant materials.

The second measurement, anterior-posterior length through the incisor, shows little variability from species to species when it is treated as a ratio to head and body length (Table 8-4). Incisor thickness to head and body length ratios for both species of Thomas Farm heteromyids fall within the range of recent heteromyid ratios, Proheteromys floridanus at 0.018, and P. magnus at 0.0147. The anterior-posterior measurement, while evidently not very informative for determining possible diet, turns out to be very highly correlated with head and body length. Calculation of a regression line of incisor anterior-posterior dimension against head body length (Table 8-1, Table 8-4), has an R^2 value of 0.98. Predicted average body

length for P. floridanus based on this measurement is 68.9 mm, and for P. magnus is 131 mm. These values are both within the range of head and body length estimates obtained using other measurements (Figure 8-6).

If incisor transverse width relative to the thickness dimension is considered, a trend begins to emerge that can be related to rodent dietary preferences (Table 8-4). The lowest ratio values (0.5, 0.6) are characteristic of seed eaters, while rodents that eat grasses and green vegetation possess wider incisors, and animals that feed on coarse roots, rhizomes, and bark have the highest transverse to anterior-posterior ratios.

The above findings suggest that the cross-sectional area of an incisor is greatest in rodents that feed on coarse vegetation, and least in seed-eating rodents that do not require massive incisors (or perhaps must have flexible incisors). This assumption can be tested by multiplying the transverse by the anterior-posterior measurement. This procedure provides the area of the smallest rectangle that would enclose a cross-section of the incisor, and is similar to the technique used by Creighton (1980) to estimate area of mammal M_1s. This measurement, while obviously an overestimate of the area, is useful for comparison. The ratios of incisor cross-sectional area to body length are shown in Table 8-4, and support the assumptions made previously. Generalists on soft vegetation, seeds, and invertebrates, for example, Peromyscus (Hamilton, 1941; Whitaker, 1966), and seed eaters such as heteromyids (Arnold, 1942; Smith, 1942; Whitaker, 1972a, 1972b; Alcoze and Zimmerman, 1973; Fleming and Brown, 1975) have ratios that range from .0125 to 0.015. Microtines (Hamilton,

1941; Birkenholz, 1972; Smolen, 1981) and other rodents such as Sigmodon that feed primarily on grasses and green vegetation (Fleharty and Olson, 1969; Cameron and Spencer 1981) have somewhat higher ratios (0.15-0.19), although there is some overlap with seed eaters. Incisors of geomyids, castorids, and erethizontids, all of which feed on roots, twigs, and bark, or use their incisors in digging (Jenkins and Busher, 1979; Rensberger, 1973), have relatively greater cross sectional area than do those of other rodents.

If a bivariate plot is constructed using the two incisor measurements that show the greatest relationship to food choice, the tranverse/anterior-posterior ratio, and the incisor cross-sectional area to head and body length, (Figure 8-7), the incisors fall into groups that can be correlated with the type of food the rodent most commonly eats. There is some degree of overlap between these groups, because although most rodents exhibit food preference, they are essentially opportunistic, and will frequently eat a wide range of food items. The incisor measurements of the two fossil species of Proheteromys from Thomas Farm indicate that these animals most likely were either seed eaters, or generalists on fairly soft vegetation, fruits and invertebrates. While all Recent species of heteromyids feed primarily or exclusively on seeds, there is no reason to assume that the fossil forms possessed such a restricted diet. Investigation of the characteristics of the cheek teeth may help to shed further light on the preferred diet of these animals.

Cheekteeth. Within the Rodentia, the diversification of cheektooth morphology has been phenomenal. Tooth evolution may be subdivided into two basic trends within the rodents:

1. Modification of cusp pattern. The change in the occlusal pattern of the tooth may progress in any one of several different directions. Starting from the "primitive" tubulosectorial pattern (Wood, 1935), retained today by some sciurids, a tooth may become more complicated by the addition of cusps, the formation of lophs, the infolding of lophs to form lakes and islands, and so on. The trend may also be seen toward simplification of the cusp pattern, so that by a very early stage of wear, the cusp pattern is obliterated. Both increased complexity of the crown and extreme simplification of the occlusal surface are thought to be adaptations for a coarser diet.

2. Change in crown height. The height of the tooth itself can increase. The trend toward hypsodonty in some cases is so extreme that the tooth becomes ever-growing. Increase in crown height is usually seen in animals that eat fairly coarse vegetation or, in the case of dipodomyines, may be related to a high metabolic rate that requires the processing of large amounts of food (Rensberger, 1973).

Assigning specific tooth morphologies to specific dietary preferences in rodents is nearly impossible. Even tooth features that hypothetically could be compared quantitatively, for example, crown height, present problems if a quantitative comparision is undertaken. Barnosky (1986) demonstrated that the ratio of the crown height to transverse width of the tooth increased during the evolution of the genus Cupidinimus. It would seem that within the Heteromyidae the measurement used be Barnosky could indicate the relative height of the

tooth. However, Liomys and Heteromys show an increase in tooth height in the occlusal regon of the tooth, an area not included in the measurement used by Barnosky, as perognathines do not show any increase in crown height in this region of the tooth. In addition, the tendency for increase in crown height may be offset by an icrease in the measurement Barnosky used as the denominator in the ratio, the transverse width of the tooth. Within dipodomyines, the tooth undergoes a great deal of increase in the transverse dimension.

A more general approach is to classify a tooth by morphological category. Occlusal patterns may be considered cuspidate, lophate, complex, and simple. Crown height may be classified as brachyodont (low-crowned), hypsodont (high-crowned), and hypselodont (high-crowned and ever-growing). The teeth of Proheteromys floridanus and P. magnus are cuspidate to lophate (with wear), and brachyodont. Even in worn teeth, the cusp pattern is usually discernable. Teeth of Proheteromys floridanus are slightly higher-crowned than those of P. magnus. These species were probably not primarily seed eaters, as their teeth are not high-crowned as are those of many of the living members of the family. However, a number of recent Perognathus species eat seeds and also possess brachyodont, cuspate teeth. The conclusion drawn is that the cheekteeth actually provide little information for pinpointing the exact diet of Proheteromys. Based on incisor morphology and tooth morphology, a reasonable proposal is that that these animals were not particularly specialized as seed eaters, although seeds may have played an important part in their diet.

Postcrania. The morphology of a postcranial element often reflects its function in locomotion. Within the Rodentia, nearly

every type of locomotion, with the exception of powered flight, is represented. The most common, "primitive" rodent morph is quadrupedal and scansorial. It is possible to trace the development of various forms of locomotion from this basic body form.

Arboreality is characterized by only slight modification of the primitive rodent morphology (Emry and Thorington, 1982, 1984). Gliding rodents, such as flying squirrels, no doubt arose from arboreal ancestors (Thorington and Heaney, 1981; Johnson-Murray, 1977). Fossorial rodents show varying degrees of skeletal modification, depending on the extent to which a fossorial mode of existence has been adopted (Hildebrand, 1985b). The trend toward saltatory, bipedal locomotion is seen a number of families, and is best-developed in the Heteromyidae, Zapodidae, and Dipodidae (Howell, 1932; Klingener, 1964).

One method of postcranial skeletal analysis involves the determination of limb ratios. As limb elements of fossil rodents are seldom complete, total length measurements, and therefore limb ratios, frequently cannot be determined directly. Prior to any analysis of the fossil rodent postcranial elements from the Thomas Farm, it is necessary to determine if limb lengths can be estimated from partial elements.

Humerus. The width of the head of the humerus, previously shown to be of use in the estimation of body size, was plotted against humerus length of quadrupedal, scansorial heteromyines. The resulting regression equation is listed in Table 8-5. Based on this regression, the average length of the humerus of Proheteromys floridanus is estimated at 9.68 mm. The accuracy of this prediction

can be checked by referring to length measurements of 10 P. floridanus humeri, complete except for proximal epiphyses (Table 8-3). Lengths of the humeri ranged from 10.63 to 11.94 mm, with a mean length of 11.22 mm. As the average height of the proximal epiphysis is just over 1 mm, the average length of a complete humerus is about 12.2 mm. This figure is over 2 mm greater than the predicted length calculated from the mean proximal head width. This discrepancy may be due to several factors. The head of the humerus of P. floridanus may be narrower in dimension with respect to length than are the proximal humeri of recent heteromyids, with the result that the predicted length based on this measurement will be short. It is also possible that the mean size of the head of the humerus does not actually represent the average size of the animal, although I made an effort to select the 50 heads measured randomly. The complete humeri values may be biased toward larger individuals, as smaller, less robust elements are more frequently broken.

In an effort to determine if the head of the humerus of Proheteromys floridanus is smaller than expected, the ratio of the average width of the head of the humerus to the average distal humeral width was calculated for recent heteromyids and for Proheteromys floridanus (distal widths do not include those of the complete humeri). The lowest ratio is seen for Dipodomys (see Table 8-6). Though this animal's humeral head is wider than expected based on its body length and body mass, the distal end of the humerus is also expanded. These characters will be discussed below. Of the quadrupedal heteromyids, the ratio for the genus Liomys is closest to that of P. floridanus. If the lengths of the humeri of Liomys are

plotted against the widths of the heads, the points fall below the regression line, indicating that this animal also has a somewhat narrower humeral head relative to humerus width than many other members of the family.

Because the length estimate of the humerus based on the average width of the head is probably less than the actual mean length, a median length was calculated, based on the length of the smallest humerus (determined by regression of the width of the smallest humeral head on humerus length) and the length of the longest complete humerus. The median length was determined to be 10.2 mm (the average estimated body length based on the width of the humerus of P. floridanus is also probably a little less than it should be--see Figure 8-3).

Radius and ulna. These limb bones break very easily and seldom are recovered intact. There are no reliable measurements that may be taken on partial radii or ulnae to predict the length of these elements. Four complete radii of Proheteromys floridanus were found, having an average length of 10.32 mm (minus distal epiphyses). These elements were among the largest radii of Proheteromys found, indicating that the more delicate and smaller size radii are not represented in this measurement (Table 8-3).

Femur. The regression of femur head width on femur length for recent quadrupedal heteromyids is listed in Table 8-5. Based on the average measurement of 100 femur heads (Table 8-3), the average predicted femur length of Proheteromys floridanus is 14.9 mm. The one complete femur of Proheteromys floridanus recovered measures 17.18 mm in total length. The predicted length of this femur, based on the

width of the femur head, is 17.05 mm. The similarity of these two measurements indicates that the length of the femur of Proheteromys can be estimated with a high degree of confidence from the width of the femur head. The estimated length of the femur of P. magnus, based on the width of one femur head (Table 8-1), is 27.5 mm.

Tibia. The length of the tibia is very highly correlated (R^2 = 0.94) with the width across the proximal end of the tibia in quadrupedal heteromyids (see Table 8-5). The predicted average length of the tibia of Proheteromys floridanus is 17.18 mm. The mean length determined from two complete tibia missing the proximal epiphyses was 16.84 mm. No specimens of P. magnus tibiae have been identified.

The above discussion shows that it is possible to estimate lengths of major limb elements from portions of the limbs. Now that this fact has been established, it is possible to pursue the question of the mode of locomotion of Proheteromys. The morphological features of the skeletal elements and the length ratios of limbs to one another will be considered in this analysis.

Vertebrae. The vertebrae of bipedal rodents are very diagnostic. The cervical vertebrae are fused in highly saltatorial forms (Hatt, 1932; Wood, 1935), as are a number of the presacral vertebrae (Hatt, 1932). No evidence of vertebral fusion was seen in either species of Proheteromys.

Humeri. The humeri of both species of Proheteromys are most similar to those of Liomys in a number of features. The greater and lesser tuberosities are not expanded as are those in other recent members of the family, the pectoral ridge is similar in length and degree of development, being longer and more robust than that of

Heteromys or Perognathus, and distal end is not particularly expanded. Hildebrand (1985b) showed that the measurement across the distal humerus divided by the length of the humerus is higher in fossorial forms than in non-fossorial animals. According to Hildebrand (1985b), the ratio is less than 30% for mammals not adapted to a fossorial mode of life. The ratios for scratch diggers range from about 30% to about 90%, depending on the degree of fossoriality. The increase is due primarily to the relative increase in width across the distal trochlea, a feature associated with greater development of the digit flexors used in digging. The ratio calculated for Proheteromys and some recent heteromyids (Table 8-6), suggests that heteromyines are not adapted for digging, although modern heteromyines do construct shallow burrows (Fleming, and Brown, 1975). The higher ratio seen in perognathines and dipodomyines is due in part to the shortening of the humerus, although the distal end of the humerus in Dipodomys is somewhat expanded as well. Dipodymines use their forelimbs in scratching for seeds, and in manipulating food (Eisenberg, 1963), which may account for development of digit flexors. Dipodomys also has expanded greater and lesser tuberosities on the head of the humerus, possibly associated with greater rotational ability of the forearm.

Ulna. The ulna of Proheteromys floridanus is very similar to that of other heteromyids, except Perognathus, which has a very gracile ulna. The ratio of the length of the olecranon to the length of the ulna distal to the semilar lunar notch has been shown to be correlated with a fossorial mode of life (Hildebrand, 1985b). A ratio of greater than 0.2 is characteristic of animals that use their

forelimbs extensively for digging. All heteromyids examined possess relatively short olecranon processes, indicating that their forelimbs are not particularly specialized for digging (Table 8-6). This conclusion is incorrect; all recent heteromyids are capable of digging and many species construct burrows.

Pelvis. The pelves of Proheteromys floridanus are not complete, so that a number of the features used to determine fossorial or bipedal mode of life are not present (Howell, 1932; Hildebrand, 1985b). The most commonly found portion, the acetabular region, is similar to that of Liomys and Heteromys.

Femur. Femora of Proheteromys floridanus are similar to those of Liomys in the morpholgy of the proximal end, and in the length and position of the third trochanter. The femur is more robust for its size than are femora of Perognathus, and the third trochanter extends farther distally on the shaft than it does in perognathines and dipodomyines. The reduction in the length of the third trochanter seen in the latter group is thought to be associated with the fusion and reduction of the adductor mass in saltatory forms. The greater trochanter does not extend as far dorsally above the head in heteromyines as it does in Dipodomys. The more dorsal placement of this structure allows for improved leverage of the gluteus medius in jumping (Howell, 1932).

Tibia. The tibiae of heteromyids are all very similar in morphology. The major difference is seen in the increase in length of the tibia of saltatory forms. This aspect will be discussed in greater detail in the section on limb ratios.

Astragalus and calcaneum. The major tarsal elements, the astragalus and calcaneum, are very similar in morphology within the recent species of quadrupedal heteromyids. In Dipodomys, several features of the calcaneum in particular may be related to saltation; the lengthening of the body of the calcaneum, the narrowing of the sustentacular surface, and the reduction in the size and development of the groove for the peroneal tendon (reduction in pronation of hindfoot). These features are associated with the restriction of movement of the hindfoot to one plane (Howell, 1932).

Limb Ratios

The postcranial anatomy of rodents of the genus Proheteromys is very similar to that of Recent heteromyines. No features associated with fossorial or bipedal means of existence are evident on any of the postcranial elements. Further evidence of a scansorial mode of locomotion can be obtained by calculation of limb ratios.

The ratios of entire length of the forelimb to the length of the hindlimb, or of segments of the forelimb to segments of the hindlimb, have been shown to be useful for determining mode of locomotion. The most commonly employed ratio, the intermembral index, compares the combined length of the humerus and radius to the combined length of the femur and tibia. Saltatorial forms possessing elongate hind limbs have lower intermembral indices than do quadrupedal forms (Wood, 1935; Howell, 1932, Emerson, 1985). Table 8-7 shows intermembral indices calculated for Recent heteromyids and for Proheteromys floridanus. Lack of limb elements prevents the determinination of intermembral indices for Proheteromys magnus. The intermembral index of P. floridanus is very similar to that of

Liomys, Heteromys, and Perognathus, and is greater than that of saltators (See Table 8-6). Among bipedal forms, Dipodomys has a considerably lower ratio than does Zapus, indicating the the proximal hindlimb segments of the latter are not as elongate. The highest intermembral index is seen in Geomys pinetis. Quadrupedal cricetids also have somewhat higher values than do scansorial heteromyids.

The revised intermembral index (Howell, 1932; Wood, 1935), is the ratio of the combined length of the humerus and radius divided by the "functional length" of the hindlimb, or the combined length of the femur, tibia, and hindfoot from the center of the ankle joint to the distal end of the longest metatarsal. Increase in length of the metatarsals is a feature of limb lengthening seen in bipedal rodents (Howell, 1932). The revised intermembral index used in this study is the combined length of the humerus and radius divided by the combined length of the femur, tibia, and metatarsal III. The ratio for Proheteromys floridanus is very similar to that for recent heteromyines and scansorial perognathines (see also Wood, 1935, Table 5), and is less than the ratios calculated for cricetids and sciurids.

If the intermembral index cannot be be calculated for a fossil form, a less informative estimate of limb ratios can be determined by dividing the length of the humerus by the length of the femur (Table 8-7). These ratios are fairly reliable means of determining mode of locomotion of an animal, although some bipedal forms, such as Zapus, do not show any pronounced modifications of the proximal limb segments, and may have humerus/femur ratios similar to those of quadrupedal rodents. In rodents highly adapted for saltatorial modes

of locomotion the length of the humerus is less than half the length of the femur.

As the length of the humerus and femur have been shown to be proportional to the breadths of their respective heads, the ratio of the head of the humerus to the head of the femur can also be used as an indicator of mode of locomotion. These ratios are listed in Table 8-7. The highest ratio, as expected, is seen in Geomys, and the lowest in Dipodomys. The ratio of Proheteromys floridanus is lower than than that of other quadrupedal rodents because as noted previously, the width of the head of the humerus is smaller than those of similarly sized recent heteromyids. The ratio of humeral head width to femur head width for recent scansorial heteromyids is similar to that of the bipedal Zapus. The latter two ratios are definitely not as informative for determining modes of locomotion as are the more complete measurements, but they may be used for estimating limb ratios of fossil rodents when only limited material is available.

Conclusions: Diet and Mode of Locomotion of Proheteromys

The information that has been compiled in the preceding pages can be summarized in a description of the fossil rodents Proheteromys floridanus and P. magnus. Proheteromys floridanus was considerably smaller than recent heteromyines, and was most similar in size to small perognathines such as Perognathus amplus and Perognathus longimembris (Hall, 1981). However, limb morphology of the fossil form indicates that it was less gracile and more heavy bodied than recent perognathines. P. magnus was very similar in postcranial morphology to Liomys, and in size was similar to Heteromys anomalus (Table 8-2).

Seeds probably were an important part of the diet of both fossil

forms, although Proheteromys may also have fed on fruits, berries, and insects. There is no evidence to suggest that these rodents fed on grasses, hard-shelled nuts, or coarse vegetation (Figure 8-7).

The mode of locomotion of Proheteromys floridanus (and perhaps of P. magnus, although sufficient postcranial material for analysis is lacking), was similar to that of modern quadrupedal heteromyids to judge from limb morpholgy, and limb ratios (Table 8-7). "Primitive" heteromyids such as Liomys exhibit, in addition to a within-pairs alternating gait (Eisenberg, 1963), a gait termed quadrupedal saltation (Bartholomew and Carey, 1954; Pinkham, 1973). In this locomotor pattern, the forelimbs strike the ground simultaneously, followed by the hindlimbs, which also move together. Quadrupedal saltation, or leaping, is also employed by several species of Perognathus (Bartholomew and Carey, 1954), but seldom by cricetines such as Peromyscus (Pinkham, 1973). The use of this gait by Liomys and the similarity of limb ratios of early Miocene heteromyines to those of recent members of the subfamily indicates that the fossil forms may also have employed this gait, and that heteromyids were perhaps preadapted for a bipedal mode of locomotion. Based on observation of feeding postures in Perognathus, Bartholomew and Carey (1954) proposed that the elongation of the hindlimb relative to the forelimb facilitated the attainment of the bipedal stance characteristic of the group. While foraging for seeds, Perognathus assumes a stance in which the body is held horizontal to the substrate while the forelimbs sift the dirt for food items. Although this is an intriguing idea, it is virtually untestable. The only reliable conclusion that may be drawn at this point is that Proheteromys

floridanus (and perhaps P. magnus) employed a means of locomotion similar to that of recent quadrupedal heteromyines.

Sciuridae

The next most common rodent family from Thomas Farm are the Sciuridae. Three species have been collected from the site, and all are being described in a separate work (Pratt and Morgan, in prep). One of the species, tentatively referred to Miospermophilus, is represented only by an M^3 and will not be discussed in this study. The majority of sciurid specimens are cheekteeth, although a small number of postcrania are known as well. Until more material is recovered, the analysis of sciurids is restricted primarily to an assessment of body size.

Sciurid Species A

The most common sciurid is a small chipmunk-like rodent that Black (1963a) assigned to Tamias. Based on newly acquired material, it appears that the animal actually belongs to a new genus that is closely related to Tamias and Eutamias (Pratt and Morgan, in prep.). The regressions of M_1 areas against body masses and head and body lengths of Recent ground and tree squirrels (Figure 8-8 and Table 8-8 and 8-9) were used to determine the size of fossil sciurids. The mean body mass of species A, based on the mean M_1 area (Table 8-10) is 22.6 gm, and the mean head and body length, 94.3 mm. The predicted size range of this species is shown in Figure 8-9. Based on these values, it appears that the small fossil chipmunk was very similar in size to the least chipmunk Eutamias minimus (Hall, 1980; Walker, 1983).

No incisors of this species have been identified. The cheekteeth are very similar to those of recent members of the genus Tamias, and provide no evidence that the diet of the fossil form was different from that of living chipmunks.

Although diagnostic postcranial remains of the fossil species are rare, several astragali have been recovered. The astragali are very similar in morphology to those of recent Tamias and Eutamias, and possess a number of characters that unite them with this group rather than with the ground squirrels, tree squirrels, or flying squirrels (Thorington and Emery, 1982; Pratt and Morgan, in prep.).

Sciurid Species B

A large, rare sciurid was tentatively identified by Black (1963a) as Prosciurus sp. The recent discovery of additional material indicates that this taxon is a member of the subfamily Petauristinae (Old World flying squirrels), and probably belongs to the genus Petauristodon (James, 1963; Lindsay, 1972; Engesser, 1979).

Based on the mean area of 3 lower molars, the predicted head and body length of species B is about 230 mm, and the predicted weight about 437 gm. The head and body length value agrees well with that predicted on the basis of one incisor with a thickness measurement of 2.99 mm (Table 8-1, 8-10). Using the regression equation for incisors in Table 8-1, the predicted head and body length is 220 mm. The estimated size range of species B is pictured in Figure 8-9. Based on the limited amount of material available, this large sciurid appears to have been similar in size to Sciurus carolinensis.

The ratio of the transverse width of the incior to its thickness, and the ratio of incisor cross-sectional area to predicted head and

body length are plotted on Figure 8-7. The point for species B falls between Tamias and Sciurus, indicating that this animal probably fed on seeds and nuts. The molars are crenulated and possess a large number of accessory cusps, but the significance of this morphology is unclear. Recent flying squirrels that possess crenulated teeth frequently feed on insects (Dolan and Carter, 1977).

The mode of locomotion of the genus Petauristodon is unknown, as no postcranial elements of this genus have been described. The examination of several astragali and calcanea recently found at Thomas Farm shows that this genus is more closely allied with the recent tree squirrels and flying squirrels than with the ground squirrels (Emery and Thorington, 1982). The gliding abilities of this animal, or lack thereof, cannot be determined until more postcranial elements are found.

The presence of at least two species of sciurids that are not closely related to spermophilines provide evidence that the region surrounding Thomas Farm in the early Miocene may have been heavily forested (Black, 1963b). This idea will be discussed further in the section on the paleoecology of the entire site.

Figure 8-1. The relationship of head and body length to body mass for Recent quadrupedal rodents. Open circles show values for bipedal rodents. Line calculated by least-squares regression; equation listed in Table 8-1.

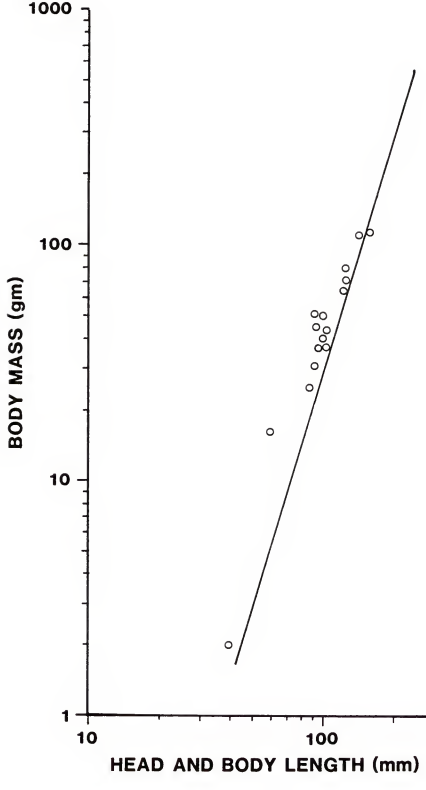
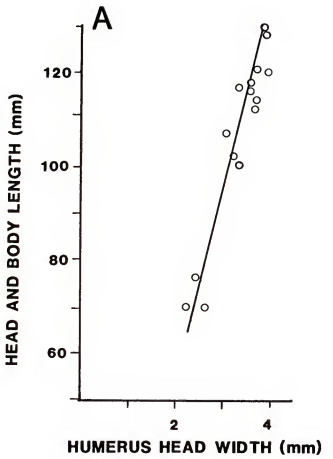

1000
100
10
1
BODY MASS (gm)
10
100
HEAD AND BODY LENGTH (mm)

Figure 8-2. The relationship of M_1 to body size in Recent heteromyids. a) Head and body length; b) Body mass. Lines fitted by least-squares regression; equations listed in Table 8-1.

A
HEAD AND BODY LENGTH (mm)
100
10
.5
1
5
$M_{\bar{1}}$ AREA (mm)^2
B
BODY MASS (gm)
10
1
.5
1
10
$M_{\bar{1}}$ AREA (mm)^2

Figure 8-3. The relationship of the breadth of of the head of the humerus to body size in Recent heteromyids. a) Head and body length; b) Body mass. Lines fitted by least-squares regression; equation listed in Table 8-1.


A
HEAD AND BODY LENGTH (mm)
120
100
80
60
2
4
HUMERUS HEAD WIDTH (mm)

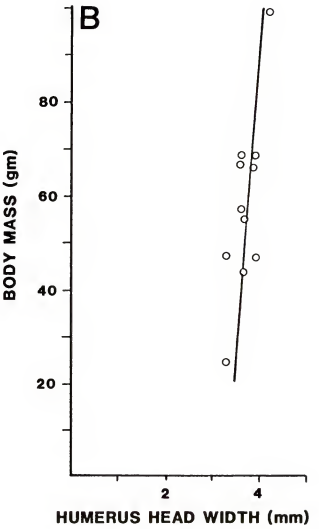

B
BODY MASS (gm)
80
60
40
20
2
4
HUMERUS HEAD WIDTH (mm)

Figure 8-4. The relationship of the width of the head of the femur to body size in Recent heteromyids. a) Head and body length; b) Body mass. Lines fitted by least-squares regression; equations listed in Table 8-1.

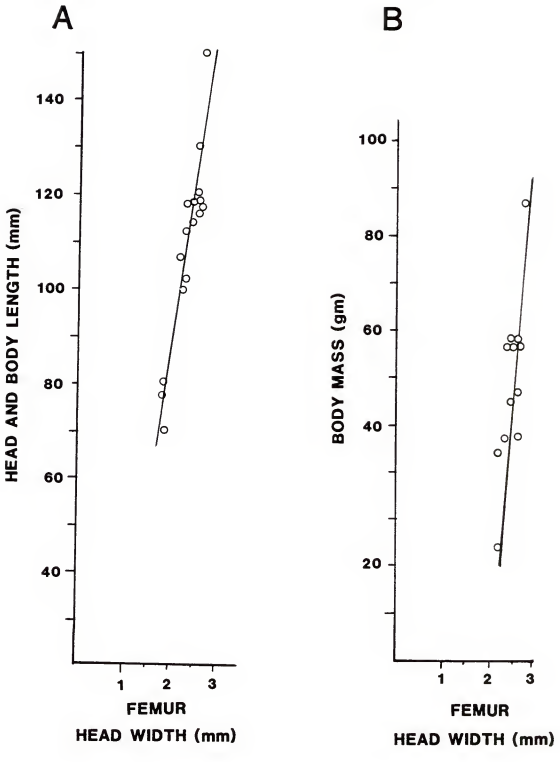
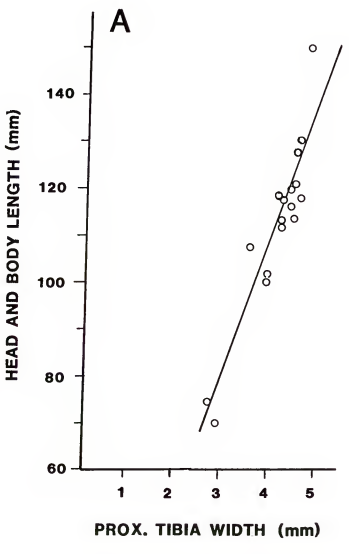

A
HEAD AND BODY LENGTH (mm)
140
120
100
80
60
40
1
2
3
FEMUR
HEAD WIDTH (mm)
B
BODY MASS (gm)
100
80
60
40
20
1
2
3
FEMUR
HEAD WIDTH (mm)

Figure 8-5. The relationship of the breadth of the proximal tibia to body size in Recent heteromyids. a) Head and body length; b) Body mass. Lines fitted by least-squares regression; equations listed in Table 8-1.


A
HEAD AND BODY LENGTH (mm)
140
120
100
80
60
1
2
3
4
5
PROX. TIBIA WIDTH (mm)

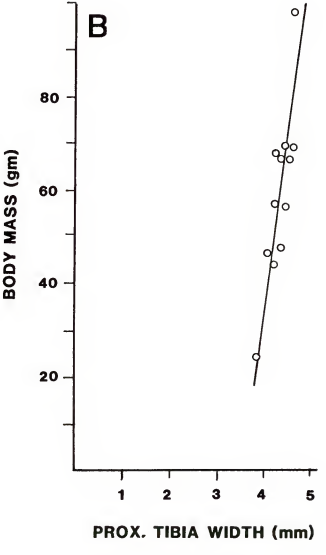
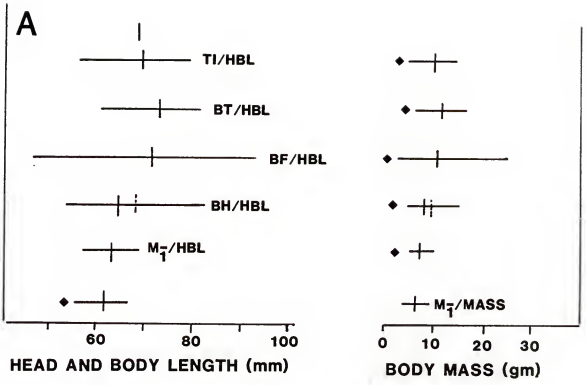

B
BODY MASS (gm)
80
60
40
20
1
2
3
4
5
PROX. TIBIA WIDTH (mm)

Figure 8-6. Body mass and head and body length estimates for a) Proheteromys floridanus; b) Proheteromys magnus. Horizontal lines indicate size range, vertical lines mark mean size, dotted lines indicate median size. Predicted size calculations determined secondarily from Figure 8-1 indicated by black diamond. See Table 8-1 for list of abbreviations.


A
TI/HBL
BT/HBL
BF/HBL
BH/HBL
M1/HBL
M1/MASS
60
80
100
0
10
20
30
HEAD AND BODY LENGTH (mm)
BODY MASS (gm)

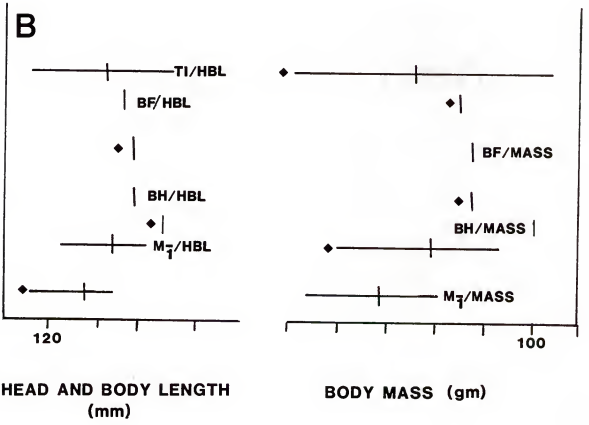

B
TI/HBL
BF/HBL
BF/MASS
BH/HBL
BH/MASS
M1/HBL
M1/MASS
120
100
HEAD AND BODY LENGTH (mm)
BODY MASS (gm)

Figure 8-7. Relationship of rodent incisor morpology to diet. Zones of overlap indicate mixed diet. Symbols: open circles, Microtinae; closed circles, Cricetinae and Hesperomyinae; open squares, Heteromyidae; closed squares, Geomyidae; open triangles, Zapodidae; closed triangles, Hystricognathi; diamonds, Castoridae; number signs, Sciuridae; asterisks, fossil Proheteromys; s, large fossil sciurid.

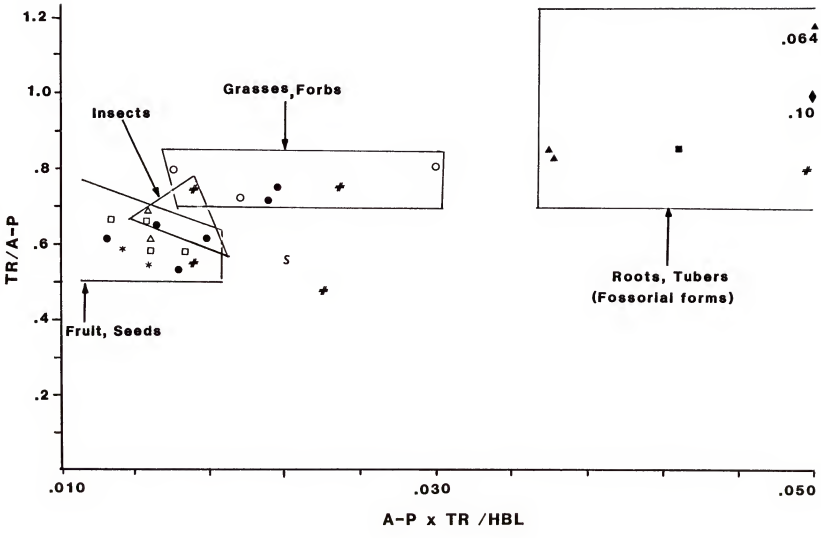
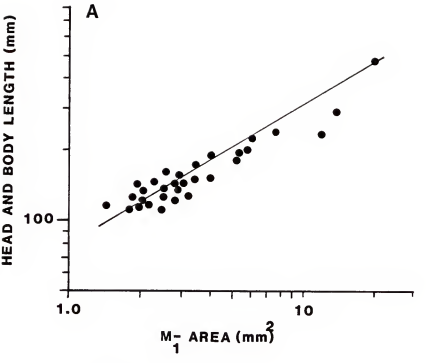

1.2
1.0
.8
.6
.4
.2
TR/A-P
Grasses, Forbs
Insects
Fruit, Seeds
Roots, Tubers
(Fossorial forms)
.064
.10
.010
.030
.050
A-P x TR /HBL

Figure 8-8. The relationship of M_1 area to body size in Recent sciurid rodents. a) Head and body length; b) Body mass. Lines fitted by least-squares regression, equations listed in Table 8-9.


A
HEAD AND BODY LENGTH (mm)
100
1.0
10
M1 AREA (mm2)

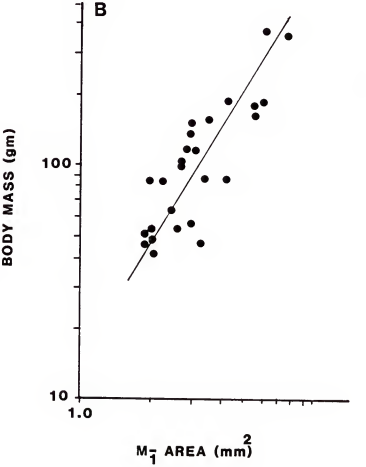
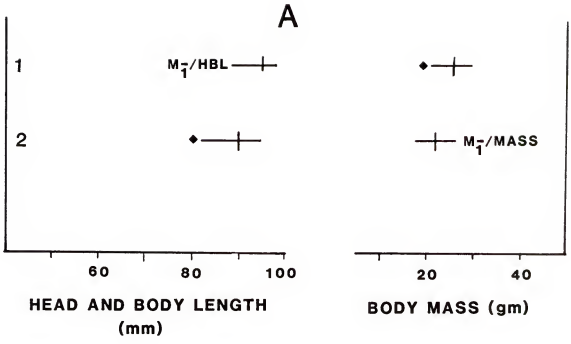

B
BODY MASS (gm)
100
10
1.0
M1 AREA (mm2)

Figure 8-9. Predicted size ranges of fossil sciurids from Thomas Farm. a) Size range of species A. 1. Head and body length calculated directly from area of M_1 regression 2. Body mass calculated directly from area of M_1 regression; b) Size range of species B. 1. Head and body length calculated directly from M_1 area regression. 2. Body mass calculated directly from M_1 area regression. 3. Head and body length calculated directly from anterior-posterior thickness of incisor regression. Diamonds indicate body size estimates based on Figure 8-1. Horizontal lines indicate range, vertical lines mark mean values. See Table 8-1 for list of abbreviations.


A
1
2
M_1^-/HBL
M_1^-/MASS
60
80
100
20
40
HEAD AND BODY LENGTH
(mm)
BODY MASS (gm)

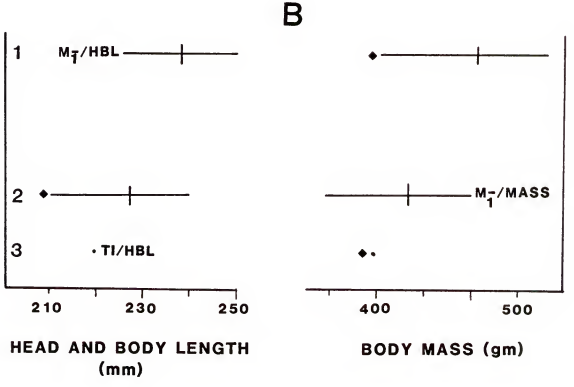

B
1
2
3
M_1^-/HBL
M_1^-/MASS
TI/HBL
210
230
250
400
500
HEAD AND BODY LENGTH
(mm)
BODY MASS (gm)

Table 8-1. The relationship of selected cranial and postcranial measurements to body size. W = body mass in grams, HBL = head and body length in millimeters, M_1 = area of M_1 in millimeters, BH = breadth of humeral head in millimeters, BF = breadth of femoral head in millimeters, BT = breadth of proximal femur in millimeters, TI = anterior-posterior thickness of incisor.

Measurements	n	R^2	Regression Equations
Body mass/Head-body Length	50	0.94	log W = 3.20(log HBL) - 4.9
M_1 Area/Body Mass	16	0.65	log M_1 = .134(log W) - .059
M_1 Area/ Head-body Length	22	0.63	log M_1 = .489(log HBL) -.83
Humerus Head/Body Mass	13	0.49	BH = .0096(W) + 3.14
Humerus Head/Head-body Length	22	0.91	BH = .0246(HBL) + .688
Femur Head/Body Mass	13	0.71	BF = .0069(W) + 2.114
Femur Head/Head-body Length	22	0.88	BF = .0142(HBL) +.756
Proximal Tibia/Body Mass	13	0.77	BT = .011(W) + 3.68
Proximal Tibia/Head-body Length	22	0.86	BT = .033(HBL) + .316
Incisor/Head-body Length	34	0.98	TI = .0119(HBL) + .37

Table 8-2. Measurements taken on cranial and postcranial elements of Recent heteromyid rodents. For list of abbreviations see Table 8-1.

Specimens	Mass (gm)	HBL (mm)	M_1 area (mm^2)	BH (mm)	BF (mm)	BT (mm)
Heteromys anomalus						
UF 6571	24.5	100		3.29	2.18	3.84
UF 6576	47.0	120		3.94	2.55	4.39
UF 6577	66.5	130		3.89	2.54	4.52
UF 13320	81.1	138	2.09			
Heteromys desmarestianus						
UF 6823	47.6	118	1.18	3.28	2.31	4.14
UF 6824	57.2	116	1.57	3.63	2.53	4.24
UF 6860	66.6	116	1.73		2.54	4.34
UF 6903	68.5	121		3.73	2.47	4.44
UF 6915	68.9	127		3.95	2.60	4.49
UF 6917	55.0	114	1.30	3.70	2.49	4.46
UF 6938	68.7	118	1.62	3.62	2.61	4.59
UF 6941	97.5	150	1.71	4.01	2.67	4.68
UF 6942	44.4	112	1.48	3.65	2.30	4.15
Liomys irroratus						
UF 6265		102	1.68	3.18	2.34	3.84
Liomys salvini						
UF 6264		107	1.49	3.00	2.18	3.52
Perognathus fallax						
UF 434	13.2	81	1.31			
UF 3035		81	1.36			
Perognathus flavescens						
UF 7835	7.5	58	1.08			
UF 8666		63	0.94			
Perognathus flavus						
UF 7833	7.7	59	1.11			
UF 7834	5.9	55	1.20			
Perognathus hispidus						
UF 11944		102	1.44			
Perognathus intermedius						
UF 7836	13.0	80	1.31			
UF 7837	15.8	80	1.30			
UF 12527		76	1.22	2.49	1.80	2.77
UF 12528		70	1.12	2.31	1.71	2.55
UF 13424	15.6	83	1.25			
Perognathus penicillatus						
UF 437		77	1.22			
UF 3040		75	1.23			
UF 4689		70	1.06	2.62	1.88	2.87
Dipodomys agilis						
UF 3056		99	2.39			
UF 429		96	1.73			

Table 8-2--continued.

Specimens	Mass (gm)	HBL (mm)	M_1 area (mm^2)	BH (mm)	BF (mm)	BT (mm)
Dipodomys merriami						
UF 4675	35.8	95	1.61			
UF 4678	42.0	94	1.78			
UF 7863		96	1.76	3.17	2.70	4.14
UF 13244	50.0	99	1.72			
Dipodomys ordii						
UF 1869			1.81	4.05	3.45	5.54
Dipodomys spectabilis						
UF 8674		117	2.54			

Table 8-3. Measurements taken on cranial and postcranial elements of Proheteromys. Abbreviations; S.D. = standard deviation of mean; C.V.(%) = coefficient of variation in percent.

Proheteromys floridanus

Measurement	n	Range	Mean	S.D.	C.V. (%)
Incisor					
Transverse width	10	0.63-0.78 mm	0.72 mm	.045	6.29
Thickness	10	1.03-1.31 mm	1.19 mm	.074	6.17
M1 Area	11	1.07-1.16 mm	1.12 mm	.038	3.39
Humerus					
Head breadth	50	1.99-2.59 mm	2.26 mm	.124	5.48
Distal width	25	2.33-2.95 mm	2.63 mm	.187	7.11
Length*	10	10.63-11.95 mm	11.22 mm	.395	3.53
Femur					
Head breadth	100	1.42-2.08 mm	1.77 mm	.121	6.82
Length	1	17.18 mm			
Tibia					
Proximal breadth	45	2.31-2.99 mm	2.72 mm	.142	5.06
Length*	2	16.20-16.84 mm	16.52 mm		
Length Metatarsal III	9	7.79-9.23 mm	8.67 mm	.523	6.04

Proheteromys magnus

Measurement	N	Range	Mean	S.D.	C.V. (%)
Incisor					
Transverse width	10	0.91-1.15 mm	1.04 mm	.072	6.92
Thickness	10	1.75-2.09 mm	1.93 mm	.109	5.65
M1 area	9	2.23-2.83 mm	2.57 mm	.172	6.70
Humerus length*	1	19.17 mm			
Femur Head breadth	1	2.71 mm			

*Missing proximal epiphyses

Table 8-4. Mean incisor ratios of Recent and fossil rodents. Abbreviatons: Tr = transverse width of incisor; A-P = Anterior-posterior width of incisor; HBL = head and body length.

Recent Species	N	Tr/HBL	A-P/HBL	Tr/A-P	A-PxTr/HBL
Heteromyidae					
Heteromys anomalus	4	.0088	.0133	.67	.0146
Heteromys desmarestianus	3	.0083	.0135	.68	.0128
Liomys pictus	3	.0094	.0160	.58	.0148
Liomys salvini	1	.0094	.0159	.59	.0160
Perognathus californicus	2	.0095	.0140	.67	.0138
Perognathus penicillatus	1	.0100	.0148	.67	.0110
Dipodomys merriami	3	.0097	.0173	.57	.0169
Geomyidae					
Geomys pinetis	3	.0154	.0178	.86	.0470
Castoridae					
Castor canadensis	2	.0120	.0120	1.00	.1001
Sciuridae					
Tamias striatus	1	.0084	.0154	.55	.0173
Cynomys ludovicianus	2	.0075	.0132	.74	.0252
Spermophilus richardsoni	2	.0078	.0105	.75	.0167
Sciurus carolinensis	3	.0072	.0145	.49	.0240
Marmota monax	1	.0097	.0126	.77	.0570
Erethizonitidae					
Erethizon dorsatum	1	.0077	.0077	.95	.0361
Octodontidae					
Spalacopus	2	.0143	.0166	.86	.0345
Ctenomys	1	.0190	.0158	1.19	.0650
Zapodidae					
Zapus hudsonicus	3	.0113	.0167	.68	.0146
Napeozapus insignis	3	.0100	.0164	.61	.0145
Cricetidae					
Microtus pennsylvanicus	3	.0093	.0128	.79	.0161
Pitymys pinetorum	2	.0140	.0197	.71	.0185
Neofiber alleni	3	.0111	.0137	.81	.0300
Sigmodon hispidus	3	.0098	.0142	.70	.0214
Oryzomys palustris	3	.0081	.0144	.56	.0162
Neotoma floridana	3	.0093	.0124	.75	.0217
Peromyscus floridanus	3	.0090	.0145	.62	.0135
Ochrotomys nuttalli	3	.0119	.0188	.62	.0176
Onychomys leucogaster	3	.0094	.0146	.64	.0149
Fossil Species					
Proheteromys floridanus		.0110	.0180	.59	.0130
Proheteromys magnus		.0077	.0147	.54	.0141

Table 8-5. Least-squares regression equations of proximal breadth of limb to limb length. Abbreviations: BH=breadth of humeral head; LH=length of humerus; BF=breadth of femur head; LF=length of femur; BT=breadth of proximal tibia, LT=length of tibia.

Measurements	N	R^2	Regression Equation
Humerus head/Humerus length	15	0.96	BH = .171(LH) + .625
Femur head/Femur length	15	0.88	BF = .075(LF) + .656
Proximal tibia/Tibia length	16	0.96	BT = .150(LT) + .145

Table 8-6. Limb ratios of recent and fossil rodents.

	Humerus		Ulna
	prox/distal	distal/length	olecranon/length
Recent Species			
Heteromys anomalus	.90	.25	
Heteromys desmarestianus	.85	.23	.17
Liomys irroratus	.86	.24	
Liomys salvini	.86	.23	.17
Perognathus fallax		.28	
Perognathus intermedius	.90	.26	.15
Perognathus penicillatus	.95	.25	
Dipodomys ordii	.83	.34	.14
Dipodomys merriami	.78	.31	.13
Fossil Species			
Proheteromys floridanus	.84	.22*	.17
Proheteromys magnus		.23	

*Average calculated from 10 complete humeri

Table 8-7. Forelimb-to-hindlimb ratios of fossil and Recent rodents. Abbreviations: IR=intermembral ratio; Rev. IR=revised intermembral ratio; LH/LF=humerus length to femur length; BH/BF= humerus head width to femur head width. See text for explanation of ratios.

Recent Species	IR	Rev. IR	LH/LF	BH/BF
Heteromys anomalus	.66	.52	.73	1.51
Heteromys desmarestianus	.65	.51	.73	1.50
Liomys irroratus	.64	.51	.69	1.36
Liomys salvini	.63	.51	.68	1.38
Perognathus intermedius	.65		.70	1.36
Perognathus penicillatus	.64	.50	.71	1.39
Dipodomys merriami	.48	.38	.51	1.17
Dipodomys ordii	.50		.49	1.17
Geomys pinetis	.78	.67	.80	1.72
Tamias striatus	.70	.58	.77	1.42
Sciurus sp.	.69*	.55*	.74*,.76	1.29
Zapus hudsonicus	.57	.43	.66	1.53
Neotoma floridana	.74+	.60+		
Peromyscus floridanus	.71	.57	.76	1.44
Fossil Species				
Proheteromys floridanus	.64	.50	.68	1.27
Proheteromys magnus			.73	

*from Wood, 1935
+from Howell, 1932

Table 8-8. Measurements taken on cranial and postcranial elements of recent sciurids.

Taxon	Head-body Length (mm)	Body Mass (gm)	M_1 area (mm^2)
Ammospermophilus leucurus			
UF 7477	141	114.2	2.84
Spermophilus spilosoma			
UF 7909	149	83.2	4.00
Spermophilus franklini			
UF 13897	223	370.0	6.00
Tamias striatus			
UF 2067	111	52.1	2.59
UF 2068	139	92.0	2.57
UF 2069	123	63.5	2.51
UF 3508	146	81.5	1.97
UF 3599	156	95.9	2.61
UF 7842	118	47.6	1.92
UF 7976	140	148.5	2.93
UF 10215	143	81.3	2.33
UF 12007	128	55.2	2.97
UF 12577	152		2.87
Eutamias amoenus			
UF 7843	128	51.5	2.05
Eutamias minimus			
UF 2496	111		2.16
UF 3606	111		1.71
UF 7134	125		1.85
Eutamias quadrivittatus			
UF 12880	114	46.0	1.86
UF 12881	118	39.5	2.05
Eutamia umbrinus			
UF 7840	114	49.7	1.96
Tamiasciurus hudsoni			
UF 4011	191	189.5	4.14
UF 4013	165	149.8	3.49
UF 4014	151	83.0	3.35
Funambulus pennanti			
UF 14595	105	55.0	
UF 14597	123	46.8	3.27
UF 15091	145	115.0	2.98
Callosciurus finlaysoni			
UF 20545	180	154.0	5.33
UF 20546	193	165.0	5.53
UF 20549	194	179.0	5.82
Funisciurus anerytherus			
UF 20569	170	180	
Cynomys ludovicianus			
UF 7828	227		12.92
UF 7829	290	1068.0	
UF 8720	292		14.72
Marmota monax			
UF 13129	468		20.57

Table 8-8--continued.

Taxon	Head-body Length (mm)	Body Mass (gm)	M_1 area (mm^2)
Sciurus carolinensis			
UF 9997	244	366	7.42
Sciurus niger			
UF 13671	300	1100 (pg)	12.6

Table 8-9. Least-squares regression equations for Recent sciurids. Abbreviatons; M_1 = M_1 area; W = body mass; HBL = head and body length.

Measurements	N	R^2	Regression Equations
M_1 Area / Head-body length	33	.95	Log M_1 = Log HBL(1.84) - 3.5
M_1 Area / Body mass	27	.92	Log M_1 = Log W(.571) - .64

Table 8-10. Measurements taken on cranial and postcranial elements of fossil sciurids. For list of abbreviations see Table 8-3.

Species A

Measurement	N	Range	Mean	S.D.	C.V.(%)
M_1 Area	5	1.2 - 1.45 mm	1.37 mm	0.09	6.6

Species B

Measurement	N	Range	Mean	S.D.	C.V.(%)
M_1 Area	3	6.6 - 8.12 mm	7.51 mm	0.65	8.7
Incisor					
Tranverse width	1	1.68 mm			
Thickness	1	2.99			

CHAPTER 9
CARNIVORA

Four families of the Order Carnivora are represented at Thomas Farm: the Canidae, Amphicyonidae, Mustelidae, and Ursidae. The absence of felids is not surprising as this family was evidently rare in North America in the early and middle Miocene (Romer, 1948; Savage and Russell, 1983). Simpson (1932) reported three carnivores from Thomas Farm, Cynodesmus nobilis, Cynodesmus (= Tomarctus) canavus, and Amphicyon sp. White (1942a, 1947) described a number of new species including canids, amphicyonids, and mustelids. Olsen (1956b) reviewed the Thomas Farm canids and showed that the majority of the species described by White were actually assignable to the species Cynodesmus iamonensis, Tomarctus canavus, and a species he called Enhydrocyon spissidens (1958a). Olsen also described the cranial (1958b) and postcranial (1960) morphology of the large amphicyonid Amphicyon longiramus, and discussed the affinities of the several "problematical" carnivores (1958a). Tedford and Frailey (1976) transferred Enhydrocyon spissidens to the genus Euoplocyon, and referred Aelurodon johnhenryi (White, 1942a) to Hemicyon (Phoberocyon) johnhenryi.

The most recent field efforts have brought to light several as yet undescribed carnivore species; however, in this chapter I will discuss the previously described carnivores only as specimens of the new forms are rare. The cranial, and when feasible postcranial, morphology of these animals will be considered, as well as estimates

of body mass. The objective of this study is to provide a picture of the carnivore guild from the Thomas Farm in terms of diet, locomotion and possible habitat preferences.

Canidae

Four canids are represented at Thomas Farm, the borophagines Tomarctus canavus and Euoplocyon spissidens, the canine Cynodesmus iamonensis, and a small as yet undescribed species that is referable to Phlaocyon or Bassariscops (H. Galiano, pers. comm.). Tomarctus canavus and C. iamonensis are the most common carnivores at the site. Euoplocyon spissidens is represented by two partial dentaries (MCZ collection), and the small canid is represented by a number of teeth and some postcranial elements.

All descriptions of Thomas Farm canids have been based on cranial material and no previous attempt has been made to assign postcranial elements to taxon. The process of identifying postcranial material to species is rendered difficult by several factors, including the lack of articulated or associated skeletons at the Thomas Farm, the rarity of complete or uncrushed elements, and the similarity in size of five of the carnivores: three canids, one amphicyonid, and one large mustelid. It has been shown that Recent canids differ little from one another in postcranial morphology (Hildebrand, 1954), and the same is true of the fossil canids from Thomas Farm.

The elements were assigned to species by the following procedure: Using measurements of identifiable cranial material as a basis, it was determined that Cynodesmus was the largest canid, and Tomarctus and Euoplocyon were smaller in size. Because cranial material of Euoplocyon is rare (no specimens in Florida State Museum

collection), all of the smaller postcrania were identified as Tomarctus, unless their morphology differed from other elements of the same type within the appropriate size range. The size range for elements of each species was determined by a threefold process. First, the ratio of the range of M_1 length of T. canavus to the total range of M_1 lengths of T. canavus and C. iamonensis combined was determined (42.6% of total range). The lower 42.6% of size ranges of skeletal elements was then initially chosen as the cutoff point for Tomarctus elements. In addition, bivariate plots of skeletal measurements were constructed as a means of determining species groupings. Attempts were also made to articulate limb elements with one another in order to assess their morphological compatibility. Predicted body masses were calculated using both cranial and postcranial elements, and the size ranges for each species based on bone measurements were compared (Figure 9-2). Once the initial separations had been made, the elements were examined for distinguishing characteristics. Although there apparently was some overlap in size ranges of T. canavus and C. iamonensis, many of the elements could be assigned to a species with a fair degree of certainty.

Cranial characteristics

Diet may be inferred by the study of cranial characters, in particular those of the dentition. Two crushed skulls of Cynodesmus and one of Tomarctus are present in the Thomas Farm collection, however distortion is so great that no total length measurements can be taken on these specimens. Fortunately, a number of partial

maxillae, mandibles, and isolated teeth of both species are available, and provide the basis for this study.

The skull of Tomarctus canavus, although crushed, appears to be quite similar in size and morphology to that of T. brevirostris from the lower Snake Creek (Matthew, 1924) in the possession of a well-developed sagittal crest and a short snout. The frontals of the Thomas Farm specimen are so damaged that it cannot be determined if they were inflated like those of T. brevirostris and more advanced borophagines (Matthew, 1924; Harrison, 1983). The orbits of both T. canavus and T. brevirostris are more posteriorly placed than are those of recent canids.

Although the teeth of T. canavus do not have the massive appearance characteristic of those of later members of the subfamily, the paracone of the M^1 is noticeably larger than the metacone, and the metaconule is well-developed. The P^4 retains a protocone, a cusp that is lost in some of the later members of the group. The length of the snout relative to that of recent and fossil canids can be demonstrated by calculating the ratio of the length of the postcanine-precarnassial toothrow (P^1-P^3) to the M^1-M^2 toothrow length (Table 9-1). The lowest ratio in living canids is seen in the one specimen of black-backed jackal Canis mesomelas measured in this study, although a number of fossil borophagines, including T. canavus, had extremely shortened muzzles. The South American bush dog Speothos venaticus actually has the shortest snout among living canids; however, the carnassial-molar length is reduced by the loss of the M^2.

The lower jaw of Tomarctus canavus is also fairly short (Table 9-1), and the teeth are robust for the size of the jaw, although they do

not appear as massive as those of T. brevirostris. The premolars possess posterior accessory cusps (Tedford and Frailey, 1976) characteristic of the subfamily. The similarity of the skull and dental morphology of late Miocene and Pliocene borophagines to that of hyaenas (Matthew, 1924; Matthew and Stirton 1930; Harrison, 1983), has led to the conclusion that members of the former group were scavengers, highly adapted for crushing bone. While there is no reason to doubt that the later, highly specialized members of the subfamily were in fact the New World equivalent of hyaenas, there is little to suggest that the early-to-middle Miocene Tomarctus was specialized as a bone-crusher. The relative shortness of the muzzle and the slightly modified cheekteeth of Tomarctus canavus do serve to indicate an ecological separation from the similarly sized Cynodesmus iamonensis. Perhaps Tomarctus canavus was a scavenger as well as an active predator.

The rare Euoplocyon spissidens has also been referred to the Borophaginae (Tedford and Frailey, 1976); however, the lack of specimens precludes any speculation on diet or preferred habitat of this canid. Although the length and width measurements of both M_1s of the species fall within the size range of those of Tomarctus canavus (Tedford and Frailey, 1976), the lower carnassials of Euoplocyon spissidens can easily be distinguished from those of Tomarctus and other borophagines by the lack of a metaconid.

The two crushed skulls of Cynodesmus iamonensis are most similar in morphology to those of Canis latrans and Canis niger. The sagittal crest closely resembles that of C. latrans, but the supra-occipital region is U-shaped rather than V-shaped, and is most similar to C.

niger. The positions of the orbit and the infraorbital foramen, the shape and thickness of the zygoma, and the width of the glenoid fossa are all very much like those of a coyote skull. The snout is considerably longer than that of Tomarctus and is much more similar in length to that of a grey fox (Table 9-1). The width of the snout cannot be determined from the complete skulls; however, a cast of a partial palate is somewhat wider than that of a coyote, and is more similar in breadth to that of a wolf.

The upper premolars and molars are very similar to those of recent species of Canis. The P^4 is slightly more massive than that of C. latrans, and possesses a labial cingulum similar to that of the wolf. The M^1 is transversely elongate (Table 9-1), and the metaconule is small to absent, unlike that of Tomarctus (Olsen, 1956b). The lower jaws and dentition of C. iamonensis are slightly more robust than those of C. latrans, but not so heavy as Canis niger. The morphology of the lower toothrow is very similar to that of Canis.

The overall similarity of the skull and dentition of Cynodesmus iamonensis to that of a coyote strongly suggests that the diet of the fossil form was comparable to that of recent members of the genus Canis. Recent Canis latrans prey extensively on small mammals, in particular rabbits and rodents (Murie, 1951; Ewer, 1973; Gier, 1975), although deer and domestic sheep may also be taken. Fruits and berries form a significant part of the diet during certain seasons of the year (Gier, 1975). Lagomorphs were absent from the early Miocene of Florida; however, rodents were abundant, as were small artiodactyls and equids. A more complete picture of the diet and

ecology of Cynodesmus iamonensis must be deferred until the postcranial anatomy and body mass of the canid are discussed.

Postcranial Morphology

The analyses of the postcranial morphology of Cynodesmus iamonensis and Tomarctus canavus are highly speculative due to the lack of associated skeletons and the rarity of complete elements. Many of the postcranial skeletal features most useful for determining means of locomotion and prey capture as well as preferred habitat require the presence of complete and associated elements (Van Valkenburgh, 1985). Without associated skeletons, a number of the elements most useful for determining mode of locomotion (in particular metapodials and phalanges) cannot be confidently assigned to species, or even to family.

Each of the major elements of Tomarctus and Cynodesmus will be considered separately in this discussion and will be compared to elements of recent canids. The postcranial anatomy and possible mode of locomotion of each canid will then be considered. Body size estimates for all carnivores will be discussed at the end of the chapter.

Axial skeleton

Hildebrand (1954) demonstrated that vertebral morphology can provide useful information concerning mode and speed of locomotion. The total length of the precaudal vertebral column can also serve as a standard measurement in the calculation of limb ratios (Hildebrand, 1952). Unfortunately, no vertebrae identifiable to the Canidae have been recovered from the Thomas Farm locality.

Scapula morphology

The morphology of the scapula is closely tied to the morphology of the musculature associated with it and the rest of the forelimb (Davis, 1949; Hildebrand 1954; Maynard Smith and Savage, 1956). Three fragmentary proximal scapulae of canids are the only portions of this element found in the FSM collection. The proximal end is the least informative portion of the scapula, and little could be inferred from an examination of the elements available.

Humerus morphology

The carnivore humerus possesses a number of features that are related to habitat preference and locomotion type (Davis, 1949; Hildebrand, 1954, 1982; Hunt, 1972). The shape of the articular head of the humerus is related to the degree of rotation of this bone at the shoulder joint. Less cursorial mammals possess more spherical humeral heads, and more cylindrical or elliptical heads are found in cursorial mammals. The latter shape is indicative of a limitation of humeral rotation and restriction of movemement to the fore-aft (sagittal) plane. The shape of the head of the humerus is fairly constant among the recent canids examined, the head of the humerus of Speothos being the most spherical. The shapes of the articular surfaces in specimens of Tomarctus and Cynodesmus are very similar to those of the grey fox and red fox.

The height of the greater tuberosity is variable within the different families of the Carnivora, but the significance of this feature is unknown. Hildebrand (1954) stated that the height of the greater tuberosity in canids cannot be correlated with degree of cursoriality. He did not discuss the shape or the position of the

lesser tuberosity, which is the site of insertion of the infraspinatus and the deep pectoral muscles. In both fossil forms, the scar for the insertion of these muscles is oriented more obliquely to the shaft than in modern canids. In Speothos, the scar for the origin of the infraspinatus runs nearly parallel to the shaft.

The distal medial epicondyle of the humerus is the site of the origin of the pronator teres. Located just distal to this region are well-defined pockets that mark the attachment of the digit flexors (Hildebrand, 1954; Hunt, 1972; Evans and Christensen, 1979). Supinators of the forepaw in canids arise from the lateral epicondylar ridge, and the digit extensors originate in this region as well. A wide distal humeral width usually indicates that these muscle groups are well-developed and that the animal possesses a fair amount of forepaw flexibility and movement. Canids adapted for a more cursorial existence do not possess a large degree of rotation of the manus, and the distal humerus is not particularly expanded (Hildebrand, 1954).

The width of the distal end of the humerus relative to the width of the proximal end provides a measure of expansion of the distal end (Figure 9-1 and Table 9-2). In the most cursorial forms, the ratio of proximal to distal width is nearly 1. The lowest ratio is seen in Speothos, which has a wide distal end, due mainly to the greater development of the medial epicondyle. Speothos is among the least cursorial of canids (Hildebrand, 1954; Langguth, 1975). The proximal/distal width ratios of the fossil canids are also listed in Table 9-1. The ratio for Cynodesmus iamonensis is similar to that of Canis niger, while the ratio for Tomartcus is slightly lower, and is most similar to that of Canis latrans and the fossil borophagine

Epicyon sp. The Pliocene borophagine Osteoborus orc has an extremely protuberant medial epicondyle, and therefore a lower proximal to distal width ratio than other canids.

The width of the trochlea-capitulum region of the humerus (from now on referred to as the trochlea for the sake of convenience) is related to the degree of rotation of the radius and lateral motion of the ulna at the elbow joint. The trochlea is narrowest in cursorial forms, as the movement of the distal limb segments are restricted to the sagittal plane (Hildebrand, 1954). Less cursorial canids possess relatively wider trochleae. The width of the trochlea often cannot be assessed by calculation of the ratio of the trochlear width to greatest distal width as both features apparently increase or decrease in size proportionally to one another (Table 9-2). However, if the width of the trochlea is divided by the width of the proximal end, the resulting ratio does reflect the width of the trochlear region. More cursorial canids such as foxes and wolves possess lower trochlea to proximal width ratios than do forms possessing a higher degree of forelimb mobility. Speothos, and oddly, Canis latrans fall into this latter group. In Cynodesmus, the width of the trochlea is greater than that of other members of the Caninae, although it is not as broad as that of Tomarctus and other borophagines (Table 9-2). Figure 9-1 shows the relationship of proximal/distal ratio to width of the trochlea/proximal width ratio. The most cursorial forms are located to the top left of the graph, the less cursorial in the lower right corner.

The length and thickness of the humerus may also indicate mode of locomotion. In general, long slender limbs are correlated with a

highly cursorial gait, and short robust limbs are associated with a less rapid, more ambulatory mode of locomotion. The ratios of the proximal and distal ends, respectively, to the total length of the humerus show that among the recent canids Speothos venaticus possesses the shortest humerus for its body size. Foxes and Chrysocyon have the longest humeri; those of wolves and coyotes are slightly shorter. The fossil canid Cynodesmus has a relatively short humerus that is most similar in relative dimensions to that of Speothos. No complete humeri of Tomarctus canavus are present in the FSM collection, however it has been reported that other borophagine dogs were relatively short-limbed compared to recent canids (Matthew, 1924; Matthew and Stirton 1930; Green, 1948; Harrison 1983). Both the fossil forms from Thomas Farm had humeri that were more robust than those of most recent canids (Table 9-2).

Radius morphology

There are five complete canid radii in the FSM Thomas Farm collection. I have assigned three of the specimens to Tomarctus canavus and two to Cynodesmus iamonensis. The fossil radii are very similar to one another, but are somewhat different in length, thickness and shape from those of most recent canids examined. As is the case with the humeri, the lengths of the radii of the fossil forms relative to other measurements are most similar to those seen for Speothos (Table 9-3). The distal end of the radius of Cynodesmus is relatively wider in its transverse dimension than is that of Tomarctus. The ratio of the proximal to the distal end of the radius of Cynodesmus is most similar to that of Chrysocyon; however the significance of this finding is not clear. The radii of both fossil

species are fairly round in cross-section, rather than flattened on the posterior surface as are those of recent canids. Although the proximal end of the radius is also more rounded in shape in the fossil forms than are those of recent canids, the configuration of the articular surface is essentially flat. This characteristic is seen in cursorial forms, and is related to restriction of the rotational ability of the radius (Hunt, 1972).

The distal radii of the fossil canids possess well-developed grooves for the tendons of the M. abductor pollicus longus, the M. extensor carpi radii, and the M. extensor digitorum communis. The morphology of the distal radius is similar to that of Canis, and is least like Speothos, in which the development of the grooves for the carpal and digit extensors is more pronounced.

Ulna morphology

The ulnae of Cynodesmus iamonensis and Tomarctus canavus are strikingly different from those of the majority recent canids examined in that they are extremely robust. The reduction in bulk of the ulna has been correlated with attainment of a cursorial mode of locomotion (Hildebrand, 1954; 1982). Three complete canid ulnae are known from the FSM collection. I have assigned 2 to Tomarctus, and 1 to Cynodesmus. Table 9-3 shows the ratios of measurements of the ulna for modern and fossil canids. In all forms, olecranon lengths relative to total ulna lengths are similar, and no specializations for digging are indicated (Hildebrand, 1982). The thickness of the distal extremity of the ulna in both Tomarctus and Cynodesmus is most similar to that of Speothos. The distal ends of the fossil ulnae are

extremely large and well-developed, with strong radio-ulnar articular surfaces.

Pelvis morphology

No complete innominates of canids have been collected at the Thomas Farm. Several partial ilia, although crushed, are similar to ilia of Canis latrans. One specimen in which the ischium is preserved has an ischiatic spine and notch almost identical to that of C. latrans, however, the ischiatic tuberosity is more massive and the relative length of the ischium is longer in the fossil form. No specimen of innominates is complete enough to allow for assignment to genus.

Femur morphology

The fossil femora are very similar to one another and no characters other than size could be found to separate Tomarctus from Cynodesmus. Three of the complete elements were assigned to Tomarctus and 1 to Cynodesmus on the basis of size. The femora of most canids are not distinct from one another for the most part, although there is some slight variation between genera. Canis and Chrysocyon possess femur heads that are oriented at a slight angle to the shaft and extend proximally above the level of the greater trochanter. Femur heads of foxes and the Thomas Farm canids are at about the same level as the greater trochanter. Jenkins and Camazine (1977) showed that the shape and several other characteristics of the femoral head can be used to determine mode of locomotion within the Carnivora. The features that they listed as most important, the shape of the articular surface of the head and the position of the fovea, are all very similar within the Canidae studied, both Recent and fossil. The

morphology of the head of the femur in the canids is related to the restriction of femur movement to the sagittal plane. The distal ends of the femora of Cynodesmus and Tomarctus are also very similar to those of modern canids in the length and development of the patellar groove, and the anterior-posterior width of the trochleae (Harrison, 1983), both features associated with maximum extension of the limb in running. As is the case with the forelimb elements, the femora of Cynodesmus and Tomarctus are somewhat shorter and thicker than those of most recent canids, except Speothos (Table 9-4).

Tibia morphology

Unfortunately, only one complete canid tibia has been collected by the FSM. This tibia is tentatively assigned to Cynodesmus, but it is in the zone of size overlap between Tomarctus canavus and Cynodesmus jamonensis. Distal tibiae of the two species are known, but they are not particularly diagnostic. The fossil forms evidently possessed somewhat wider distal tibiae than recent forms, and the tibia is relatively shorter than those of most recent canids (Table 9-5). As Hildebrand (1954) stated, the morphology of the canid tibia provides little information related to mode of locomotion so it will not be discussed in detail.

Fibula morphology

No complete fibulae of canids are known from the Thomas Farm. The partial fibulae are robust, and the distal ends are large. There is little indication of reduction in size of the fibula seen in later forms, nor is there any evidence that the distal fibula was fused to the tibia is it is in some modern canids. The reduction in thickness of the fibula and the tendency for it to be closely bound to the tibia

distally are both modifications for rapid locomotion (Hildebrand, 1982) that had not been achieved by either Cynodesmus or Tomarctus.

Limb Ratios

An extensive analysis of limb proportions in the Canidae was undertaken by Hildebrand (1952) to elucidate taxonomic standing and mode of locomotion of various recent taxa. Although many of the ratios that Hildebrand discussed cannot be determined in this study, there are several limb ratios that provide some information concerning the mode of locomotion of the Thomas Farm canids.

Forelimb ratios

Hildebrand (1952) determined that the greatest difference in relative forelimb length between taxa is due primarily to variation in the length of the radius relative to the humerus and metacarpals. The most cursorial canids possess longer radii than humeri, while those that are not particularly adapted for a cursorial gait possess relatively short legs, with radii shorter than humeri. Table 9-6 lists the radius to humerus length ratios for recent and fossil canids. The data were obtained from Hildebrand (1952), and from measurements of skeletons in the FSM Mammalogy collection. The ratio for Cynodesmus iamonensis is based on the few complete specimens known, the ratio for Tomarctus robustus is taken from Hildebrand's (1952) analysis of a skeleton described by Green (1948). The relative shortness of the forelimb of Cynodesmus indicates that although the limbs of this animal possessed a number of the canid modifications associated with a cursorial mode of existence, it was probably not a fast runner, and not adapted for open terrain. It is likely that Tomarctus also had a shorter radial length relative to humerus length,

as most borophagines whose limbs have been analyzed were considerably less cursorial in morphology than were members of the Caninae (Harrison, 1983).

Hindlimb ratios

According to Hildebrand (1952), the ratio of the length of the tibia to that of the femur is not as highly correlated with cursoriality as is the forelimb ratio. The ratio of tibia to femur length for Cynodesmus does serve to reinforce the observation that this canid possessed extremely short limbs (Table 9-6). The forelimb/hindlimb ratio has been shown to be of little use in determining mode of locomotion in canids (Howell, 1944; Hildebrand, 1952).

Locomotion of Tomarctus canavaus and Cynodesmus iamonensis

The two most common canids from the Thomas Farm locality, although possessing different cranial features, were very similar in postcranial morphology. Their short and robust limbs were not suitable for a highly cursorial mode of locomotion; however, a number of the characteristics seen in more cursorial canids were present in the skeletons of both forms. Their overall postcranial body form appears to have been most similar to that of Speothos, which is adapted for life in highly vegetated streamside environments (Hildebrand, 1954; Langguth, 1975). Hildebrand showed that limb ratios of the later Tomarctus robustus were similar to those of the dhole Cuon, however no skeletons of Cuon were available for comparison in this study. The possibility that no early Miocene canids had achieved a high degree of cursoriality, and that the short limbs of Tomarctus and Cynodsesmus are primitive rather than

specialized features, must also be considered (Ewer, 1973). More study of the evolution of Miocene carnivore faunas is needed before this question can be resolved. At any rate, the observation that these canids were probably not good runners implies that they would not have been successful predators in situations requiring pursuit over open ground, and may have had to rely on stealth and ambush as a method of obtaining prey. If the fossil forms did indeed employ this type of prey capture, then the area surrounding the Thomas Farm was probably covered by vegetation and was not open grassland.

Amphicyonidae

Two members of the family Amphicyonidae are known from Thomas Farm: the small Cynelos caroniavorus, and the huge Amphicyon longiramus. Neither species are as abundant as the canids, but Amphicyon longiramus is moderately common.

Cynelos caroniavorus is represented by a few specimens of cranial and postcranial material. The only skull portion known is an MCZ specimen of a maxillary fragment with molars. An isolated M^1 and several partial lower jaws are known, including one nearly complete specimen, a mandible with P_3 through M_2. The lower jaw is similar in size and shape to that of a red wolf, although the premolar/molar ratio is somewhat longer in Cynelos (Table 9-1). The lower carnassial appears very small relative to the length and thickness of the jaw. The lack of a complete dentition makes it difficult to speculate on the possible diet or feeding habits of Cynelos caroniavorus. The upper carnassials of European species of Cynelos (Ginsberg, 1966) possesses a large protocone, although shear between carnassials was evidently well-developed. The P_4 of members of the genus is small,

and the M_1, although short, possesses a somewhat bulbous talonid. Cynelos caroniavorus was obviously at least partially carnivorous, although the type of food taken is unknown.

Postcranial material of Cynelos caroniavorus is also rare. The only elements in the FSM collection assignable to this species are a distal humerus, two proximal radii, and a proximal tibia. The distal end of the humerus possesses an expanded knob for the origin of the pronator teres muscle (Hildebrand, 1954; Evans and Christensen, 1979). The expansion of the distal humerus indicates that the pronators and supinators of the manus were probably well-developed (Hunt, 1972). The trochlea is also wide, as evidenced by the ratio of trochlear to distal width (.74) which is greater for Cynelos than for any species of recent or fossil canid (Table 9-2). The width of the trochlea indicates that range of motion at the elbow was probably quite extensive. The shallowness of the distal humerus in the anterior-posterior direction and the shallowness of the olecranon fossa are characteristic of mammals that do not extend the limb fully. All the features discussed above are characteristic of an animal that is not highly cursorial, but is more ambulatory in mode of locomotion.

The radius of Cynelos caroniavorus is similar to that of Cynelos sp. described by Hunt (1972). The proximal articular surface has a spiral configuration that, as Hunt demonstrated, is related to an ambulatory gait in mammals such as bears. The more complete radius of C. caroniavorus also possesses a ridge-like radial tuberosity and a pronounced scar that marks the attachment of the lateral collateral ligament. These features were also seen on the radius of Cynelos sp. described by Hunt (1972).

The morphology of the proximal tibia provides little information that may be of use in determining mode of locomotion; however, based on the morphology of the fragmentary forelimb elements, it appears that C. caroniavorus was not at all adapted for cursorial locomotion. The evidence available suggests that this animal had a more ambulatory mode of locomotion, and possessed a fair degree of dexterity of the forepaws. In this respect it differed from the canids at Thomas Farm.

The cranial and postcranial skeleton of Amphicyon longiramus has been described in detail by Olsen (1958b, 1960) and will not be extensively treated here. The skull and dentition of this animal have been described as being more canid-like than bear-like (Olsen, 1958b). The carnassials have not lost their shearing capacity, and the molars are not as expanded as are those of omnivorous-herbivorous species. It has been proposed that Amphicyon may have been a scavenger, or adapted for crushing bones (Olsen, 1958b); however, the premolars are not enlarged like those of true bone crushing forms such as borophagine dogs and hyaenas. The extremely long jaw also provides some evidence that this animal's jaw muscles probably could not generate the power needed to crush bone. The absence of a large felid at the site provides the best indication that Amphicyon longiramus may have been filling the large carnivore niche, and feeding on the abundant ungulates that frequented the area.

Olsen (1960) described the postcranial morphology of Amphicyon longiramus in considerable detail, and little can be added to the study save for a few corrections and a cautionary note. Although the species is represented by several complete limb elements, it is likely that some of them actually belong to the ursid Hemicyon

johnhenryi that is also known from the Thomas Farm site. Separating the elements on the basis of size is nearly impossible, as Amphicyon longiramus, like other members of the genus, was apparently sexually dimorphic (Ginsberg, 1961) and the size range of Hemicyon falls within the lower end of the size range of Amphicyon longiramus.

In his description of the skeleton of A. longiramus, Olsen (1960) described and figured several elements that actually belonged to Hemicyon johnhenryi. The most notable of these is the scapula, which possesses a postscapular fossa and is very similar to that of modern bears (Davis, 1949). Olsen commented on on the resemblance of this element to that of recent bears, but did not realize that the specimen was not that of an amphicyonid. One large, crushed scapula of Amphicyon longiramus has been prepared recently, and it also possesses a postscapular fossa.

If Olsen's identification of the other elements of the skeleton are accepted as belonging to Amphicyon, a few additional observations may be made that provide information on the possible mode of locomotion of this large carnivore. The distal humerus possesses a greatly enlarged knob for the origin of the pronator teres, and the scar for the ligament of the supinator is evident on the lateral epicondylar ridge. These muscle groups (pronator and supinator of the front paw) were evidently well-developed. The morphology of the distal humerus is similar to that described by Hunt (1972) for the large amphicyonid Ysengrinia. No complete humeri of A. longiramus are known from the FSM collection, so a more complete comparison cannot be made at this point.

The ulna is massive and bear-like, particularly in the region of the semi-lunar notch. The expansion of the lateral articular surface of the notch in bears is related to greater degree of lateral movement at the elbow joint. The proximal radius possesses the spiral configuration discussed above that is associated with a high degree of lateral rotation of the elbow.

The metacarpals and phalanges are large, and not elongate; however, the configuration of the foot is unlike that of bears in which the 3rd, 4th, and 5th metacarpals are all about the same length. The configuration of the metacarpals is more canid-like, with the 3rd metacarpal being the longest. Although Olsen identified isolated phalanges to digit, I do not regard these identifications with any confidence. In addition, the medial phalanges that he described and figured are those of a camelid and not a carnivore (1960:39).

The hindlimb, in particular the femur, is long and fairly slender. The ratio of the average length of the tibia to that of the femur is 0.88, which is lower than the tibia/femur ratios of modern and fossil canids, but is about 10% higher than the ratio of these elements seen in Recent and fossil bears (Emslie and Czaplewski, 1985). The metatarsals are short and robust, and the third metatarsal is longer than the other more lateral metatarsals.

Amphicyon longiramus may have been bear-like in its method of movement. The presence of postscapular fossa on the scapula implies this animal may have also had the ability to climb trees (Davis, 1949). A thorough study of the postcranial morphology and degree of sexual dimorphism in Amphicyon longiramus must be undertaken before firm conclusions can be drawn.

Ursidae

The presence of Hemicyon (Phoberocyon) johnhenryi at the Thomas Farm marks the earliest known occurence of Hemicyon in the New World (Tedford and Frailey, 1976). Cranial material of the species consists of one mandible, of which the Florida State Museum has a cast (the original belongs to the MCZ). The jaw is much shorter than that of Amphicyon longiramus, although the teeth are as large. The M_1 is more elongate than that of Amphicyon, especially in the shearing portion of the trigonid, and the tooth is narrower. The P_4 is larger than that of Amphicyon. No upper teeth of this species are known, although later forms of Hemicyon possess dentitions reminiscent of those of modern bears (Matthew, 1907). The dentition and shape of the jaw of Hemicyon johnhenryi is most similar to that of borohphagine dogs, and the specimen was originally assigned to the canid genus Aelurodon (White 1947). It is likely that this animal was more adapted for carnivory than for omnivory.

The only postcranial elements definitely assignable to Hemicyon johnhenryi include a scapula, a calcaneum, and an astragalus. The scapula possesses a number of ursid characters. The highly developed postscapular fossa is particularly interesting, as in modern ursids this structure is associated with development of the muscles used in anchoring the forelimb in climbing (Davis, 1949; Olsen, 1960). Whether H. johnhenryi possessed the ambulatory gait of recent bears or was more cursorial cannot be determined from the material available.

Mustelidae

Three species of mustelid have been described from Thomas Farm; the large Oligobunis floridanus (White, 1947), the otter-sized

Leptarctus ancipidens (White, 1941; Olsen, 1957a and b), and a small form that Olsen (1956a) referred to Miomustela. Tedford and Frailey rejected Olsen's identification of Miomustela and stated that the Thomas Farm species was a true musteline, most similar to a European form, "Plesictis" juleni (Viret, 1929). Tedford and Frailey rejected this name also as the genoholotype of Plesictis is not a mustelid but a procyonid (Hough, 1948). The proper identification of "Miomustela" must await a revison of the group. In addition to the three described mustelids, at least one undescribed species, intermediate in size between "Miomustela" and Leptarctus ancipidens is present at the locality. Unfortunately, the material is fragmentary and a positive identification cannot be made at this time.

Oligobunis floridanus. This large mustelid is rare at the Thomas Farm locality. The only identified specimen is a lower mandible in the MCZ collection. Based on the lower jaw only, a limited number of conclusions may be drawn concerning the mode of life of O. floridanus. The relatively slender M_1 with its trenchant talonid indicates that this animal was highly carnivorous, and may have fed on small mammals such as rodents.

Among the postcrania, only a proximal humerus in the FSM collection can be confidently assigned to Oligobunis. The humerus is relatively long and not particularly robust. The deltoid and pectoral ridges are not highly developed as are those of some recent mustelids such as Taxidea and Lutra.

Leptarctus ancipidens. Several nearly complete skulls of this unusual mustelid have been recovered from the Thomas Farm, but very little postcranial material can definitely assigned to this species.

Characteristics of the skull include a short snout, paired parasagittal crests, and a rugose temporal area (Qiu and Schmidt-Kittler, 1982). The zygomatic arch is extremely wide, the small orbit is bounded posteriorly by well-developed postorbital processes. The upper cheekteeth are fairly robust; the P^3 is conical, and the P^4 possesses a large anterocone and hypocone, such that carnassial shear is reduced. The M^1 is subquadrate in outline.

The lower jaw is short and robust. The ventral edge of the jaw angles upward at the level of the M_2. This feature has been described as a subangular lobe by Qiu and Schmidt-Kittler (1982), but bears little ressemblance to the subangular lobe on jaws of the canids Urocyon and Otocyon. The lower dentition of L. ancipidens is chararacterized by a P_4 with distinct accessory cusps, and a large M_1 with distinct entoconid, hypoconid, and hypoconulid. The M_2 is larger than that of many recent mustelids and is double-rooted (Olsen, 1957b).

Qiu and Schmidt-Kittler (1982) speculated on the food habits of Leptarctus, stating that the lack of a single median sagittal crest on the skull and the presence of a subangular lobe on the lower jaw were indicative of a highly insectivorous diet. These conclusions were based primarily on presumed similarities of the crania of leptarctines to that of the bat-eared fox Otocyon, which has a diet consisting primarily of insects (Ewer, 1973). The jaw adductor muscles of Otocyon, in particular the temporalis, are not powerful, and do not originate from the top of the skull. For this reason, the sagittal crest is lacking and the origin of the temporalis is marked by two ridges located more laterally on the braincase. The temporal region

is rugose. The lower jaw possesses a large subangular lobe just below the angular process. This lobe reportedly acts to change the direction of action of the depressor mandibulae, a modification also associated with a more insectivorous diet (Ewer, 1973). These features are seen on the crania of Urocyon as well, which does not feed primarily on insects (Guilday, 1962; Stains, 1975; Trapp and Hallberg, 1975).

I contend that Leptarctus was not insectivorous, and that the features cited by Qiu and Schmidt-Kittler are not necessarily associated with an insectivorous type of diet. The double parasagittal ridges on the skull of Leptarctus ancipidens are strong and high, and are located quite close to the dorsal midline of the skull. The rugosity of the temporal region is characteristic not only of foxes, but is seen on skulls of mustelids such as Taxidea as well, and is probably not a reliable character for indicating dietary preferences. The most convincing evidence for the presence of powerful jaw adductor muscles in Leptarctus is provided by the wide zygomatic arch and well-developed postorbital processes. A wide zygoma and well-protected orbit are seen on the skulls of animals that possess strong temporalis muscles (Ewer, 1973). A deep scar on the anterior-lateral surface of the zygoma probably marks the site of origin of the superficial masseter, a muscle that exerts an upward and forward pull on the lower jaw. In mammals with weakly developed temporalis and masseter muscles, the zygomatic arch is slender and post-orbital processes are absent (Ewer, 1973). The shape of the lower jaw is no doubt related in part to directions of muscle pull,

but the lack of a true subangular lobe indicates that the depressor mandibulae may not necessarily be affected.

The dentition of Leptarctus ancipidens is more robust than that of highly carnivorous forms like Martes, and the carnassials are not as adapted for shearing as are those of some of the hypercarnivorous mustelids. Olsen (1957a) noted the general similarity of the dental and cranial morpholgy to that of Taxidea, although the teeth and lower jaws of L. ancipidens are not as robust or heavy as those of a badger. This cranial resemblance to a badger leads to the speculation that Leptarctus may have been badger-like in its eating habits, preying on small to medium size rodents (Ewer, 1973).

The comparison of the fossil form to a badger raises the question if, like a badger, Leptarctus ancipidens was fossorial. There is little evidence to support or disprove this idea, although the one distal humerus tentatively assigned to this species is very similar to those of Taxidea and Lutra. The distal humerus is shallow, with a wide, well developed medial epicondyle and medial condylar foramen. At the present time, evidence against a fossorial mode of life is all negative--examination of all carnivore distal phalanges in the Thomas Farm FSM collection did not turn up any specimens that appeared to be expecially modifided for digging (Hildebrand, 1982).

Very little information is available concerning "Miomustela" and the undescribed mustelid. The former is very mink-like in dental morphology (only lowers known). The M_1 has a reduced metaconid and trenchant talonid. The weasel Mustela vison has a lower dentition similar to that of the fossil form, and feeds on small mammals, crayfish, and frogs seasonally (Ewer, 1973; Gerell, 1967). The

material of the undescribed species is too fragmentary to allow for any description of dental or postcranial morphology.

Body Sizes of the Thomas Farm Carnivores

Body mass of each of the known carnivores from Thomas Farm was determined using the Zooarchaeology Program (ZAP) available through the FSM Zooarchaeology Department. The predictive equations used for canids and mustelids were based, respectively, on measurements of recent canids and mustelids. Canid regressions were used to estimate the size the small amphicyonid, and the Carnivora regression was used to determine body size of Hemicyon and Amphicyon. The measurements used to calculate body mass of the fossil carnivores and the regression equations are available through the FSM Zooarchaeology Department.

Canidae Body Size

Body mass estimates for canids are shown in Figures 9-2 and 9-3. The body masses predicted using the length of the lower carnassial are much higher than the estimates based on postcranial measurements. This discrepancy is probably due to the fact that the length of the M_1 is not as highly correlated with body mass as are a number of the postcranial measurements. The predicted body masses for Tomarctus and Cynodesmus based on the various postcranial features are all quite similar to one another. According to these results, T. canavus was about the size of a red fox (Eisenberg, 1981) or a black-backed jackal (Beckoff, 1975), ranging in body mass from about 7.3 kg to 11.5 kg. Small individuals of Cynodesmus jamonensis overlapped slightly in size with large individuals of T. canavus, while large members of this species exceeded 17 kg in weight. These animals were similar in size to the coyote (coyote size ranges from Gier, 1975; Eisenberg, 1981).

No postcrania of Euoplocyon spissidens are known, but judging from the length of the lower carnassial, these canids were approximately the same size as Tomarctus canavus.

Amphicyonidae and Ursidae Body Size

The body mass of an amphicyonid is difficult to estimate, as no closely related living species are available for comparison. Using the least-squares regression equations for recent canids (ZAP program), body masses estimates fro Cynelos caroniavorus range from 15 to 23 kg (large coyote to small wolf size).

Body mass of Amphicyon longiramus was estimated using the regression equations constructed from measurements of a wide array of recent carnivores. Although there is a large degree of spread in the predictions, the majority of predicted body masses are found in the 70 to 100 kg size range (Figure 9-3). The American black bear Ursus americanus has body mass range simiar to that estimated for A. longiramus.

The predicted body mass of Hemicyon johnhenryi was based on only a few specimens. The estimates range from 54 to 98 kg. More fossils of this species must be found before the size range can be estimated accurately.

Mustelidae Body Size

Body mass estimates for the mustelids were based on the measurement of the depth of the lower jaw below the M_2. As shown in Figure 9-3, there was little overlap in the size ranges of these smallest carnivores. "Miomustela" was similar in size to recent members of the genus Mustela, and was evidently slightly smaller than Mustela vison. Leptartus ancipidens was smaller than Taxidea or

Lutra, but larger than Martes martes. Oligobunis was a very large mustelid with a body mass greater than than that of the badger, Taxidea (modern mustelid size data from Eisenberg, 1981).

Size Ranges of the Thomas Farm Carnivores

Figure 9-3 shows that among the most common carnivores at Thomas Farm there was actually very little size overlap, but there was an almost constant range of size from the smallest to largest carnivore. The limited amount of size overlap implies that the carnivores were perhaps partitioning prey on the basis of size. Rosenzweig (1966) has shown that prey selection by sympatric carnivores over 2 kg in mass is correlated with predator body mass. Based on his findings, it is likely that the rodents from the locality were the preferred prey of the the mustelids and the small canid Tomarctus, while Cynodesmus may also have taken larger prey items. Assuming that Amphicyon longiramus was also primarily carnivorous, the small horses and artiodactyls from the site were suitably sized prey.

Figure 9-1. Plot of proximal/distal breadth (BP/BD) ratios of humerus against trochlea/proximal breadth (BT/BP)ratios. Single points represent 1 individual, thin lines represent observed range of values for a species, dark boxes represent 1 standard deviation on either side of mean. Abbreviations: C.d., Canis dingo; Ch, Chrysocyon; C.l., Canis latrans, C.n., Canis niger; Cy, Cynodesmus; Du, Dusicyon; Ep, Epicyon; Os, Osteoborus; To, Tomarctus; Ur, Urocyon; Vu, Vulpes.

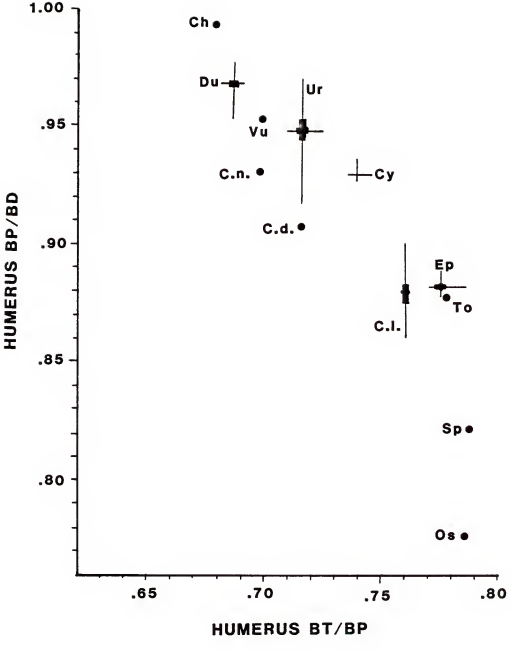
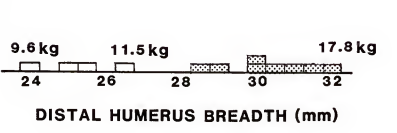
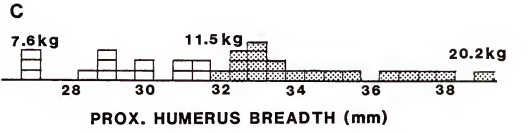
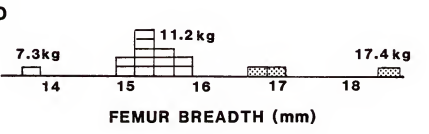

1.00
.95
.90
.85
.80
HUMERUS BP/BD
.65
.70
.75
.80
HUMERUS BT/BP
Ch
Du
Ur
Vu
C.n.
Cy
C.d.
Ep
To
C.l.
Sp
Os

Figure 9-2. Frequency-size distribution of selected measurements of elements of fossil canids. Body mass estimates based on least-squares regressions of skeletal measurements against body mass for Recent carnivores. a) Length of lower carnassial; b) Breadth of proximal humerus; c) Breadth of distal humerus ;d) Breadth of femur head; e) Greatest length of calcaneum. Shaded blocks represent Cynodesmus jamonensis, white blocks represent Tomarctus canavus, black blocks represent Euoplocyon spissidens. Each block represents one individual.

A
12.9kg
19.9kg
32.4kg
16
18
20
22
M_7 LENGTH (mm^2)


B
9.6kg
11.5kg
17.8kg
24
26
28
30
32
DISTAL HUMERUS BREADTH (mm)


C
7.6kg
11.5kg
20.2kg
28
30
32
34
36
38
PROX. HUMERUS BREADTH (mm)


D
11.2kg
7.3kg
17.4kg
14
15
16
17
18
FEMUR BREADTH (mm)

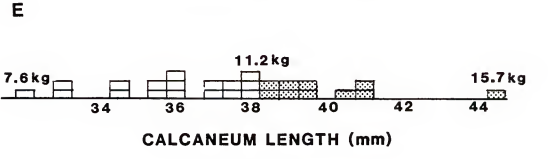

E
11.2kg
7.6kg
15.7kg
34
36
38
40
42
44
CALCANEUM LENGTH (mm)

Figure 9-3. Estimated adult body mass ranges of Thomas Farm carnivores. a) Carnivores less than 25 kg; b) Carnivores greater than 20 kg. Abbreviatons: Am, Amphicyon; Cynd, Cynodesmus; Cynl, Cynelos, He, Hemicyon; Le, Leptarctus; Mi, Miomustela; Ns, new mustelid species; Ol, Oligobunis; To, Tomarctus.

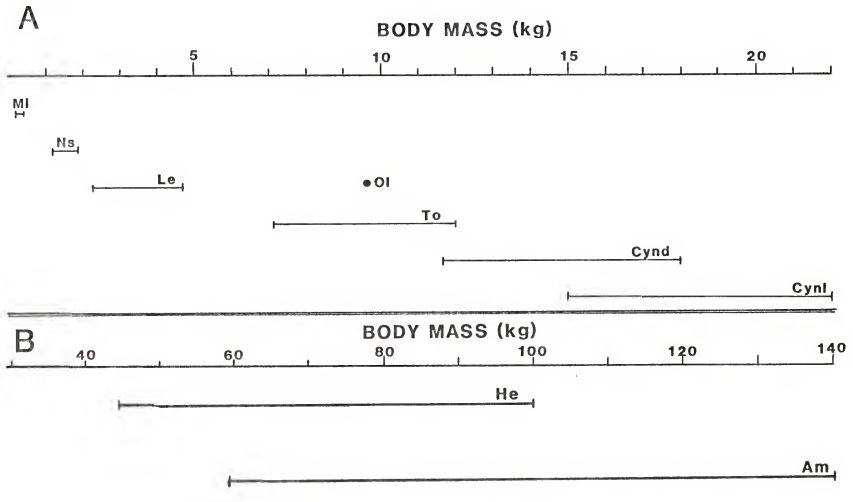

A
BODY MASS (kg)
5
10
15
20
MI
Ns
Le
Ol
To
Cynd
Cynl
B
BODY MASS (kg)
40
60
80
100
120
140
He
Am

Table 9-1. Cranial ratios of fossil and recent canids and fossil amphicyonids.

Species	p^1-p^3/p^4-M^2	P_1-P_4/M_1-M_3	M^1 length/width
Speothos venaticus	.93	1.45	.83
Urocyon cineroargenteus	.92	1.23	.73
Vulpes vulpes	1.06	1.46	.68
Fennecus zerda	.93	1.23	.65
Dusicyon sechurae	.87	1.22	.81
Chrysocyon brachyurus	1.11	1.49	.78
Canis latrans	1.01	1.22	.76
Canis niger	.82	1.08	.77
Canis dingo	1.01		
Canis mesomelas	.71	.94	.73
Cynodesmus jamonensis	.91	1.33	.68
+Tomarctus canavus	.67	1.04	.74
+Tomarctus brevirostris	.70		
+Epicyon sp.	.63		
+Aelurodon saevus	.65		
+Osteoborus sp.	.72		
*Cynelos caroniavorus		1.14	

+Fossil canids
*Fossil amphicyonids

Table 9-2. Ratios of selected humerus measurements of recent and fossil canids. Abbreviations: BD, distal tranverse breadth; BT, tranverse breadth of trochlea; L, total length; Th, minimum thickness of shaft. See Chapter 2, p. 26 for description of measurements.

Taxon	BP/BD	BT/BD	BT/BP	BP/L	BD/L	Th/L
RECENT						
Speothos venaticus	.82	.65	.79	.20	.25	.076
Urocyon cineroargenteus	.97	.69	.71	.17	.17	.072
Vulpes vulpes	.95	.66	.69	.15	.16	.063
Dusicyon sechurae	.95	.64	.67	.15	.18	.067
Chrysocyon brachyurus	.99	.68	.68	.16	.16	.059
Canis latrans	.87	.66	.76	.18	.20	.071
Canis dingo	.91	.65	.72	.18	.19	
Canis niger	.93	.65	.69	.19	.20	.079
FOSSIL						
Cynodesmus jamonensis	.94	.67	.74	.21	.24	.082
Tomarctus canavus	.87	.69	.77			
Epicyon sp.	.89	.66	.77			
Osteoborous orc	.78	.60	.78			

Table 9-3. Ratios of selected measurements of canid radii and ulnae. Abbreviations: LU, length of olecranon; ThU, anterior-posterior thickness of ulna distal to semi-lunar notch. See Table 9-1 for list of other abbreviations, and Chapter 2, p. 26 for descriptions of measurements.

	RADIUS				ULNA	
Taxon	BP/BD	BP/L	BD/L	Th/L	LU/L	ThU/L
RECENT						
Speothos venaticus	.85	.15	.18	.089	.20	.106
Uroycyon cineroargenteus	.74	.09	.13	.067	.14	.086
Vulpes vulpes	.77	.09	.12	.057	.14	.081
Dusicyon sechurae	.75	.11	.14	.070	.15	.090
Chrysocyon brachyurus	.67	.08	.11	.053	.13	.074
Canis latrans	.76	.11	.14	.075	.16	.092
Canis niger	.72	.11	.16	.082	.17	.093
FOSSIL						
Cynodesmus lamonensis	.64	.13	.19	.078	.18	.104
Tomarctus canavus	.72	.13	.18	.074	.16	.108
Epicyon sp.	.73	.12	.16	.083		
Osteoborus orc	.70	.13	.18	.084		

Table 9-4. Ratios of selected measurements of canid femora. Abbreviations: BH, breadth of femur head. See Table 9-1 for list of abbreviations and Chapter 2, p. 26 for descriptions of measurements.

Taxon	BH/BP	BP/L	BD/L	Th/L
RECENT				
Speothos venaticus	.49	.24	.20	.089
Uroycyon cineroargenteus	.43	.21	.18	.071
Vulpes vulpes	.45	.19	.16	.073
Dusicyon sechurae	.48	.20	.16	.075
Chrysocyon brachyurus	.44	.19	.14	.057
Canis latrans	.45	.22	.17	.069
Canis niger	.47	.23	.19	.072
FOSSIL				
Cynodesmus lamonensis	.47	.22	.19	
Tomarctus canavus	.45	.22	.20	.080

Table 9-5. Ratios of selected measurements of canid tibiae. See Table 9-1 for list of abbreviations and Chapter 2, p. 26 for description of measurements.

Taxon	BP/BD	BP/L	BD/L
Speothos venaticus	1.49	.22	.15
Urocyon cinereoargenteus	1.39	.17	.12
Vulpes vulpes	1.44	.15	.10
Dusicyon sechurae	1.57	.15	.10
Chrysocyon brachyurus	1.55	.14	.09
Canis latrans	1.51	.18	.12
Canis niger	1.51	.20	.13
+Cynodesmus iamonensis	1.44	.19	.14

Table 9-6. Forelimb and hindlimb ratios of modern and fossil canids.

Taxon	Ratio Radius/Humerus
Speothos venaticus	.79
Urocyon cineroargenteus	.95
Vulpes vulpes	.98
Dusicyon sechurae	.88
Chrysocyon brachyurus	1.04
Canis latrans	1.01
Canis niger	1.03
Cynodesmus iamonensis	.85
+Osteoborous cyonoides	.94*
+Epicyon sp.	.98
	Tibia/Femur
Speothos venaticus	.96
Urocyon cineroargenteus	1.06
Vulpes vulpes	1.12
Dusicyon sechurae	1.11
Chrysocyon brachyurus	1.09
Canis latrans	1.02
Canis niger	1.05
+Cynodesmus iamonensis	.90

+fossil species
*data from Harrison, 1983.

CHAPTER 10
UNGULATE PALEOECOLOGY
Perissodactlya

Equidae

Simpson (1932) reported three equids from Thomas Farm: Parahippus leonensis, Archaeohippus nanus, and the anchitheriine Anchitherium clarenci. White (1940, 1941, 1942a, 1947), evidently misled by the wide size range of specimens of the sexually dimorphic Parahippus leonensis (Hulbert, 1984), named several additional horse species on the basis of size. Bader's quantitative study of the Thomas Farm equids (1956) showed that only two species of small horse were present at the site, Parahippus leonensis, and Archaeohippus blackbergi. Hulbert (1984) supported Bader's findings concerning P. leonensis.

Analysis of Parahippus leonensis.

The small horse P. leonensis is the most abundant large mammal (as opposed to microvertebrate) at the Thomas Farm locality. Figure 10-1, compiled from the total recent ungulate sample of major bone-bearing layers, shows that in terms of abundance of individuals, this animal dominated the ungulate fauna. An extensive analysis of the paleoecology of P. leonensis was undertaken by Hulbert (1984), and little new information can be added to his findings. Specimens collected subsequent to Hulbert's study will be included in the analysis.

Population dynamics. Life history and population studies have been undertaken for several species of fossil ungulates (Kurten, 1953,

Voorhies, 1969; Hulbert, 1982, 1984). The Thomas Farm sample of Parahippus leonensis was originally chosen as a suitable subject for construction of a life table because it met several of the requirements for this type of an analysis. The sample size was sufficiently large, and the fossils had evidently been deposited during a relatively short time interval, geologically speaking. Hulbert's dynamic life table analysis (1984) was based on tooth wear classes of 89 dentaries from the MCZ and FSM collections. The most recent excavation has resulted in the recovery of additional mandibles of P. leonensis, 24 of which are assignable to age classes.

Hulbert (1984:550) plotted crown heights of the M_1 against crown heights of the M_2 to illustrate that the Thomas Farm specimens of P. leonensis could not be placed into discrete age classes. It has previously been stated by Voorhies (1969) and Kurten (1953), that births within a population must be seasonal, and deposition must be catastrophic, or if the bones within a deposit are accumulated attritionally, deaths must occur seasonally, for discrete age classes to be detected. The assemblage is almost certainly attritional, therefore even if births did occur seasonally, this feature of the Thomas Farm population of Parahippus could not be discerned.

The revised life table (Table 10-1) is nearly identical to that published by Hulbert (1984:555), and supports his conclusion that the assemblage was attritional. As the sample of jaws used in the construction of the original and the revised table was obtained from the site as a whole, it cannot be definitely determined if deposition within any one sedimentary layer occurred seasonally. Unfortunately, the number of jaws with complete locality data are not numerous enough

to allow construction of separate life tables for any of the layers. One difference between Hulbert's findings and the most recent life table is the higher correction factor for juveniles in this study. The underrepresentation of first year individuals is probably due in part to the rapidity with which carcasses of young are destroyed (Voorhies, 1969; Hulbert, 1982, 1984).

Sexual dimorphism. Molar lengths of 15 jaws were measured and the results added to Hulbert's data (1984:556) to produce the histogram shown in Figure 10-2. Hulbert's conclusion that the population of Parahippus leonensis was sexually dimorphic is supported by the revised data. Hulbert proposed that the social structure of early Miocene equids such as Parahippus may have been similar to that of modern forest-dwelling artiodactyls, in which competition between males occurs during the breeding season only (Eisenberg, 1981). While this suggestion is mainly speculation, the fact that Recent horses are not sexually dimorphic in size implies that social behavior patterns of early equids were different from those seen today in recent equid populations.

Body mass. Body weight estimates of Parahippus leonenis have been published in several previous studies. Hulbert (1984) estimated the weight of P. leonensis to be from 50 and 70 kg, based on skull condylar width and femur head width (least-squares regressions from Martin, 1980). M_2 area was used to predict a head and body length of 1.2 meters (least-squares regression from Creighton, 1980). Janis (1982) estimated the mass of Parahippus (no species given) as 80 kg, based on an unpublished regression of M^2 area to body mass of ungulates. MacFadden (in press) constructed a number of body mass

regressions using data obtained from cranial measurements of Recent equid specimens. Based on a number of measurements taken on Thomas Farm fossils, he estimated that the body mass of P. leonensis was 70-80 kg, and averaged about 76 kg. All of the above estimates show a high degree of similarity, indicating that the fossil equid was roughly the size of Odocoileus virginianus (Eisenberg, 1981).

Diet and habitat. Several studies have addressed the subject of the evolution of ungulate faunas in North America, and have shown that by the late Miocene, North America was dominated by savanna-adapted forms (Webb, 1977, 1983; Janis, 1982, 1984). The development of savanna environments has been attributed to a climatic trend of increasing aridity in the Miocene. By the late Miocene, the North American equid fauna was diverse, and composed predominantly of hyposodont, cursorial forms (Janis, 1984). Although Janis (1984) asserts that the trend toward advanced, grassland-adapted forms was well underway by the early Miocene and even the late Oligocene, the Thomas Farm equid fauna does not appear to reflect this trend. Parahippus leonenis was a relatively small horse with fairly low-crowned teeth and three functional toes on each foot. It has been pointed out that P. leonensis does show a number of dental characteristics associated with transition from a herbaceous to a more fibrous diet, several of which are also seen in earlier equids, including molarization of the premolars, complication of molar morphology, and the presence of cement on permanent premolars and molars (Bader, 1956; Janis, 1984; Hulbert, 1984). That P. leonensis was not fully adapted for a fibrous diet is indicated by a fairly low hypsodonty index of 0.94 (Figure 10-3), placing the teeth of this

animal in the brachyodont range, well below the hyposodont placement of late Miocene equids (Janis, 1984). Hulbert (1984) calculated annual cheektooth wear rates of P. leonensis, and showed that rates were about halfway between those of hypsodont grazing equids and brachyodont browsing artiodactyls. The features of the dentition of P. leonensis indicate that this animal may have been feeding on a combination of leafy vegetation and more fibrous grasses (Hulbert, 1984). Janis (1976) stated that the ability of modern equids to exist on a low-quality fibrous diet is related in part to their large body size (and hence relatively lower metabolic rate than smaller artiodactyls). It is probable, given the digestive physiology of equids, that an equid of small body size, particularly one with fairly brachyodont teeth, could not process enough low-quality food at a rate sufficient to sustain its metabolic requirements.

Analysis of Archaeohippus blackbergi

The small equid Archaeohippus blackbergi is not as common at the Thomas Farm locality as Parahippus leonensis, although it is the second most abundant large herbivore. Unlike P. leonensis, this species has not been the subject of in-depth paleoecological analysis. Sufficient material is known to allow preliminarily analysis of the population dynamics of A. blackbergi. This study will be undertaken at some future date.

Sexual dimorphism. Bader (1956) found no evidence of size-related sexual dimorphism based on Archaeohippus blackbergi cranial or postcranial measurements. Recently collected mandibles as well as those already present in the FSM and MCZ collections were measured in an attempt to detemine if a bimodal distribution of measurements could

be detected. Measurements of lower molar toothrow length were plotted on a histogram (Figure 10-2b), but the sample size is too small to provide any evidence of absence or presence of sexual dimorphism within the population.

Body mass. Several estimates of the body mass of Archaeohippus blackbergi have been presented in the literature. MacFadden (in press) estimated that A. blackbergi weighed between 39.6-40 kg, and averaged about 43 kg. Janis (1982) reported a mean weight of 25 kg for the genus. The predicted head and body length based on average area of the M_1 (tooth measurement data from Bader, 1956) using Creighton's regression (1980) is about 75 cm. This length is similar to that of recent Mazama mazama, which has an average weight of about 17 kg. Using Martin's (1980) regression of femur head width against body weight, the range in predicted body size based on measurements of 15 femora is 29-46 kg, with a mean of 39 kg. The range of estimated weights is wider than that of Parahippus leonensis. In the absence of agreement between the various predictions, MacFadden's is accepted as the most reliable, as his regression equations are based on equids only and the others are based on a number of mammalian groups. The femur head width provides an estimate that agrees well with that obtained in in MacFadden's study, therefore it seems reasonable to conclude that Archaeohippus blackbergi weighed 30-45 kg.

Diet and habitat. The dentition of Archaeohippus blackbergi lacks some of the advanced features characteristic of the teeth of Parahippus leonensis. The molars are more brachyodont (Figure 10-3), and lack cement (Bader, 1956). The small size of this equid (about 1/2 to 2/3 the size of P. leonensis), coupled with a relatively

unspecialized equid dentition, indicate that Archaeohippus was restricted to a non-fibrous, herbaceous diet, and was probably a woodland-dwelling form. A more complete analysis of dietary preferences must await SEM tooth studies.

Analysis of Anchitherium clarenci.

Remains of Anchitherium clarenci are relatively rare, and little is known about this species. Body size estimates range from 110 kg for the genus (Janis, 1982) to 160 kg (MacFadden, in press). The teeth of Anchitherium clarenci are extremely brachyodont (Figure 10-3) and lack cement. The anchitheriines were primarily European in their distribution, and these forms have been described as forest-dwelling browsers (Simpson, 1932; Janis, 1984).

Rhinocerotidae

Specimens of rhinoceroses from Thomas Farm are rare in the FSM collection; most of the described material is in the MCZ collection. In the course of the most recent excavation, only a few elements of rhinos were found. Near the completion of the field portion of this study, a deep trench was excavated in the northern part of the site, exposing a layer rich in well-preserved rhinocerotid remains. Examination of photographs taken during the 1956 Harvard University field season indicates that this layer, dubbed the "rhino level" by workers, was also encountered by the MCZ crew when a deep drainage trench was dug in the northern part of the site. The presence of rhinos in one level of the site is intriguing, because the remains of other vertebrates are not concentrated primarily within any one layer. This problem cannot be solved at this time--more excavation of the

lower bone-bearing sediments is needed before any conclusions can be drawn as to the significance of this finding.

Wood (1964) published a thorough description of the two rhinocerotids from Thomas Farm. He compared the size of the larger form Floridaceros whitei with that of the black rhinoceros, which can exceed 1,000 kg in mass (Eisenberg, 1981). According to Wood, Floridaceros has a rather primitive dentition. The limb elements are about the length of those of a black rhino, but Wood (1964) felt that their relatively slender morphology was an indication that this large animal was cursorial, much like the smaller Subhyracodon.

Diceratherium barbouri was much smaller in size than Floridaceros. Janis (1982) provided a body mass figure of 220 kg for the genus Diceratherium. Wood described the teeth as more hypsodont than those of Floridaceros. The limbs of this form were long and slender, indicating a cursorial mode of locomotion (Wood, 1964). The presence of two cursorial rhinos at the site seems to imply that open terrain was not far from the locality. Janis (1982) suggested that the Miocene rhinocerotids, like their present-day counterparts, fed on leafy browse in an open woodland-grassland habitat. Recent black rhinos frequent woodland edge habitats with permanent water sources (Frame, 1980).

Artiodactyla

Eight species of artiodactyl have been reported from Thomas Farm. Although the artiodactyl fauna is diverse compared to the equids, no one species of artiodactyl is particularly abundant at the locality. Several of the forms are rare and have yet to be identified to species. As with the Thomas Farm carnivores, many of the artiodactyl

postcranial remains are unidentified. The three camel species are all quite similar in size, and their postcrania (in particular the limb elements) appear very similar to one another. A complete description of locomotion in these animals must await analysis by an expert in the field. The two moschids, Blastomeryx floridanus and Machaeormeryx gilchristenensis are sufficiently different in size and morphology from other artiodactyls and from each other to allow identification of their postcranial elements. An investigation of these forms is currently in progress by another worker, so their postcranial morphology will not be discussed in detail here.

Tylopoda

Three species of camelid have been described from Thomas Farm. Simpson (1932) described Oxydactylus floridanus and White (1940, 1941, 1942a, 1947) named several genera of camelids. Maglio (1966), and Patton (1967), reidentified Oxydactylus floridanus and two species described by White (1941, 1947) as Nothokemas floridanus. Maglio (1966) erected a new subfamily, the Floridatragulinae, and assigned several species originally described by White to the species Floridatragulus dolicanthereus. Patton (1967, 1969) maintained that two species, F. dolichanthereus, and F. barbouri, were present at the site. Maglio (1966) also noted the presence of a third large camelid that was more advanced than either Floridatragulus or Nothokemas. Material was insufficient to allow a complete identification. Since that time, more material of this animal has been recovered, but specimens are relatively rare compared to those of the other forms. The protoceratid Prosynthetoceras texanus (Patton, 1967, 1969) was originally described by White as two separate species, Syndoceras

australis (1941), and Synthetoceras douglasi (1947). The protoceratids were originally placed in the Ruminantia (Patton, 1967, 1969), but later studies have shown this family to be a member of the Tylopoda (Patton and Taylor, 1971; Webb and Taylor, 1980).

Analysis of the Camelidae

Cranial material of camelids is relatively rare in the FSM collection, and much of it is in very poor condition. If measurements of crown heights could not be taken on complete specimens, isolated teeth were also included in the analysis. Nothokemas floridanus is the larger of the two described camelids. Its teeth are among the most hypsodont of all the ungulates known from the site (Figure 10-3), although by Janis' standard (1984), this camel's dentition was relatively brachyodont. N. floridanus probably weighed in the region of 100 kg (Janis, 1982). N. floridanus has been placed in the Aepycamelinae by some workers. The advanced members of this group were apparently similar to giraffes in their feeding habits, adapted for eating vegetation of upper tree branches. Janis (1982) proposed that early members of this group, while not as specialized as later forms for high-level browsing, may have been selecting leafy vegetation above ground level.

Floridatragulus dolicanthereus was smaller than Nothokemus and possessed relatively low-crowned teeth (Figure 10-3). It has been noted (White, 1942a; Maglio, 1966; Patton, 1967), that Floridatragulus had an extremely long, slender snout. Janis(1982), based on morphological analysis of early Miocene camelids and Recent forms, suggested that brachyodont camelids with long tubular snouts were highly selective in choice of food, and browsed near ground level for

tender plants and leaves. Their narrow snouts allowed them to select the plant items they found most appetizing. Janis described these animals as adapted for an open woodland-grassland habitat. The low abundance of Floridatragulus at the Thomas Farm locality may indicate that the region directly surrounding the sinkhole was not its optimal habitat, but that more open territory was located somewhere nearby.

Analysis of the Protoceratidae

No skulls of Prosynthetoceras texanus have been recovered from the Thomas Farm, but specimens of this species found in Texas possess both rostral and postorbital horns (Patton, 1969; Patton and Taylor, 1971). According to Figure 10-1, 8% of the recently collected Thomas Farm ungulate fauna is composed of this species, however, this number is based on fragmentary postcrania which may be misidentified. Janis (1982) estimated that members of the genus Prosynthetoceras weighed about 80 kg. The teeth of P. texanus are brachyodont, but are among the most high-crowned teeth of all the ungulates known from the locality (Figure 10-3). Janis (1982) discussed the cranial morphology of Prosynthetoceras and suggested that members of this group, which possessed broader muzzles than many of the other artiodactyls of the time, may have fed on non-fibrous semi-aquatic vegetation, or browsed on young leaves. The presence of elaborate horns led Janis to speculate that the social structure was based upon year-round, male-defended feeding and breeding territories. Certain members of the genus, such as P. texanus, were entirely subtropical in their distribution (Patton and Taylor, 1971), and are thought to have been adapted for woodland habitats (Janis, 1982).

Ruminantia

Two members of the suborder Ruminantia are known from the Thomas Farm, Blastomeryx floridanus (White, 1940, 1941; Maglio, 1966; Patton, 1967) and Machaeromeryx gilchristensis (White, 1941; Maglio, 1966; Patton, 1967). These small artiodactyls were first assigned to the Cervidae (Patton, 1967), and later placed in the Moschidae (Webb and Taylor, 1980).

Analysis of the Moschidae

The minute Machaeromeryx gilcristensis and the somewhat larger Blastomeryx floridanus were apparently hornless, and possessed brachyodont cheekteeth (Figure 10-3). Janis (1976, 1984), proposed that small fossil ruminants weighing under 15 kg, like their recent counterparts, were not able to process fibrous vegetation and therefore their diets consisted of the most tender vegetation available. The modern analogs of the fossil forms are hornless, non-territorial species that live in densely forested regions (Janis, 1982). M. gilchristensis was extremely small; size estimates based on femur head width (Martin, 1980) range from 2 to 3 kg, similar to the mass of Recent Tragulus (Janis, 1984). These small artiodactyls may have been prey of the canid Cynodesmus iamonensis .

The larger Blastomeryx floridanus was probably also restricted to a diet containing little in the way of fibrous vegetation. The teeth of this form are similar in crown height to those of M. gilchristensis (see Figure 9-3). The size of Blastomeryx has been estimated at 15-20 kg by Janis (1982, 1984). In terms of raw abundances, the two moschids represent over 16% of the total unuglate fauna. Their abundance provides evidence that the region surrounding the Thomas

Farm sinkhole was forested, with sufficent tender vegetation to sustain two populations of small brachyodont artiodactyls.

Other Groups

Two species of artiodactyl are among the rarest members of the large vertebrate fauna at the Thomas Farm. The tayassuid Desmathyus olseni was described by White (1942), and an isolated tooth of an oreodont was assigned to Merychyus sp. by Maglio (1966). Specimens of both taxa are so rare that they cannot be discussed fully in this study. Recent excavations have resulted in the recovery of several fragments of a second, larger tayassuid.

Analysis of the Merycoidodontidae

Oreodont remains from Thomas Farm consist of a few isolated teeth and tarsal elements, and examination of these fossils provides little information concerning oreodont mode of life and habitat preferences. However, this taxon deserves some mention, as its rarity at the locality has been cited as an indicator of climate and environment in the Miocene of Florida (Romer, 1948). Romer suggested that the lack of oreodonts, which he considered forest-dwelling animals (Romer, 1948:10), provided evidence that during the early Miocene, Florida was a fairly arid, grass-covered plain. Janis (1982) compared oreodonts to the Asian deer Axis axis, maintaining that the fossil forms were entirely folivorous, and existed in mixed-sex groups in open woodlands. Herds of the recent Axis are constantly on the move, selectively feeding on suitable vegetation in one area before traveling on to another. For this reason they are locally abundant at different times in different areas. Janis suggested that the large numbers of oreodonts in some fossil localities (particularly those

that formed under catastrophic conditions) reflects similar feeding and social behaviors of oreodonts.

The low numbers of oreodonts at Thomas Farm does not necessarily indicate that wooded areas were absent in the region during the period in which the deposit was being formed. These animals may never have been locally abundant in the area, and in fact may never have attained great numbers in Florida. Faunal studies of other early Miocene localities from Florida are needed in order to resolve this question.

Conclusions: The Thomas Farm Ungulate Fauna

In considering the entire group of ungulates from the Thomas Farm locality, several points should be noted. If the fauna is compared with that of the late Miocene of North America (Janis, 1984:99) the differences in the compositions of the faunas are quite evident. The ungulates from Thomas Farm were all brachyodont-to-mesodont, and the majority of the species weighed less than 200 kg. The late Miocene fauna was composed predominantly of hypsodont forms, many of which attained large size. The smallest forms all showed extreme development of hypsodonty. Thomas Farm is similar to other early Miocene faunas in the relatively low diversity of equids. In the late Miocene, equids dominated ungulate the fauna in terms of number of species. This trend can be seen in Florida; seven species of equid have been reported from the late Miocene Love site (Hulbert, 1982), as opposed to three from Thomas Farm.

The predominance of ungulates adapted for woodland or open woodland environments at the Thomas Farm locality indicates that in this region, the transition to a savanna-grassland environment was not yet underway in the early Miocene. It must be remembered that the

fauna sampled by the deposit was evidently very localized, as opposed to a fauna sampled in a stream deposit, which often contains animals from a wide variety of habitats. A more complete picture of early Miocene environments in Florida can only be obtained by additional studies of similarly aged sites.

Figure 10-1. Relative abundances of ungulate taxa from combined units 5 through 11. Percentage values obtained by dividing MNI per species by total MNI of ungulate fauna (n = 102). Abbreviations: An, Anchitherium; Ar, Archaeohippus; Blast, Blastomeryx; Mach, Machaeromeryx;, Me, Merychyus; No, Nothokemas; Para, Parahippus; Pro, Prosynthetoceras; Rh, Rhinocerotid; Ta, Tayassuidae; ?, unidentified camelid.

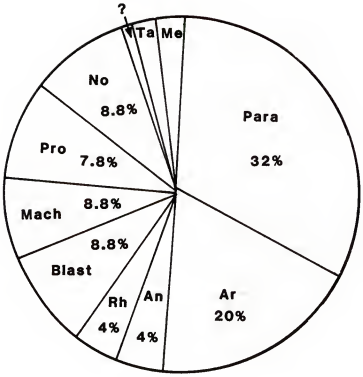
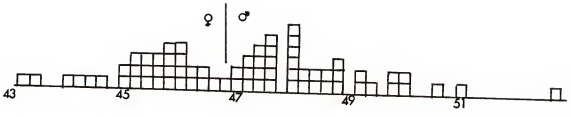

?
Ta
Me
No
8.8%
Para
32%
Pro
7.8%
Mach
8.8%
8.8%
Blast
Rh
4%
An
4%
Ar
20%

Figure 10-2. Histograms showing lower molar lengths (M_1-M_3), in mm, for Thomas Farm equids (some data from Hulbert, 1984). Each square represents one individual. a) Parahippus leonensis; b) Archaeohippus blackbergi.

A



B

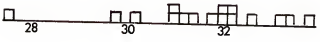


Figure 10-3. Area of M^1 plotted against hypsodonty index for selected Thomas Farm ungulates. The hypsodonty index is obtained by dividing the unworn crown height of the M_3 by the anterior-posterior length of the M_2 (Janis, 1984). Abbreviations: An, Anchitherium; Ar, Archaeohippus; B, Blastomeryx; F, Floridatragulus; M, Machaeromeryx; N, Nothokemas; Pa, Parahippus; Pr, Prosynthetoceras.

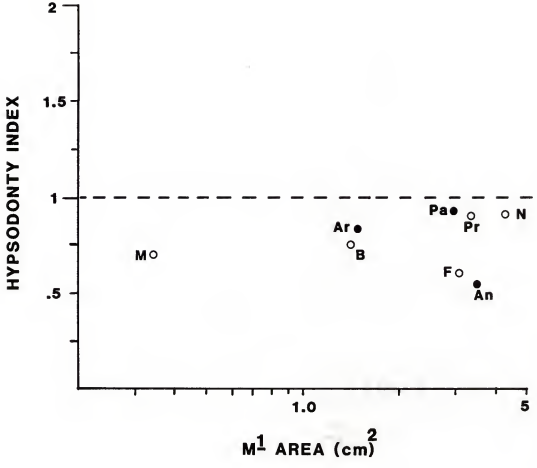

2
1.5
1
.5
HYPSODONTY INDEX
Pa
Pr
N
Ar
B
M
F
An
1.0
5
M1 AREA (cm2)

Table 10-1. Life table for the Thomas Farm population of Parahippus leonensis (based on Hulbert, 1984). A juvenile underrepresentation factor of 15.67 was used in the calculation for wear-class 1. The minimum number of individuals (MNI) for each wear-class was multiplied by 7.042 to produce cohorts whose original size was 1000 individuals. Abbreviations: d_x, number of individuals of a cohort that die within the duration of wear-class x; l_x, number of survivors out of the original 1,000 to survive to the beginning of wear-class x; q_x, the fraction of individuals who die during wear-class x ($=d_x/l_x$).

Wear class	(MNI) d_x	$7.0242d_x$	l_x	q_x
1	47	331	1000	.331
2	6	42	669	.063
3	12	86	627	.136
4,5	18	127	542	.234
6	18	127	415	.306
7	21	147	288	.510
8	17	120	141	.851
9	3	21	21	1.000

CHAPTER 11
CONCLUSIONS: COMMUNITY ANALYSIS

The final procedure in a taphonomic and paleoecological reconstruction of a fossil assemblage involves an analysis of the composition of the living community. In the broad sense, a community is defined as a group of populations of living things in the same place (Krebs, 1972). Based on this definition, an analysis of a present day community would be impossible. Most ecologists limit their studies to various taxonomic subsets of the total community, such as the plants, birds, or mammals, or regional subsets, such as boreal forest community, river community, and so on. In a fossil assemblage, community analysis must be restricted to those taxa which are best represented and will provide the most information. The Thomas Farm reconstruction will emphasize the mammaliam fauna for a number of reasons. First, the mammals are the best-known class from the site. Second, the majority of community studies on Recent environments that will be used as comparative studies also deal mainly with mammals.

The loss of information that occurs in the passage of a community from a living state to a fossil assemblage and from a fossil assemblage to a collection limits the type and amount of community reconstruction that can be undertaken. A number of relationships investigated by modern ecologists, in particular competitive interactions and predator-prey relationships, are among the subjects that can never be treated fully in a paleoecological study.

Parameters that can be discussed are relative abundances and densities of members of the fauna, basic trophic relationships, and environmental and climatic reconstruction. These analyses can be undertaken with confidence only if the worker possesses a clear picture of the taphonomic processes involved in the formation of the site.

Mammalian Abundances

The study of the number of individuals within a species is an issue of most ecological studies (Andrewartha and Birch, 1954). Abundances of animals can be discussed either as relative values, or as densities per a given area in the habitat. Mammalian population density has been shown to be related to body size (Mohr, 1940; Harestead and Bunnell, 1979; Eisenberg et al, 1980; Peters and Raelson, 1984; Robinson and Redford, 1986), habitat and latitude (Eisenberg, 1980; Peters and Raelson, 1984), diet, (Eisenberg, 1980; Peters and Raelson, 1984; Robinson and Redford, 1986), and indirectly related to metabolic rate (McNab, 1980) and home range (McNab, 1963; Harestead and Bunnell, 1979; Damuth, 1981).

Estimation of the living population densities of animals represented only by fossil remains is extremely difficult because the abundances of fossils never accurately reflect the population densities of the animals in life. Biases are introduced even before fossilization begins. In an attritional assemblage, such as Thomas Farm, the initial bias against animal abundances representing true population densities is caused by differential death rates. Hypothetically, over a period of time, more skeletons of small animals are available for fossilization than those of large animals, simply

because small mammals have shorter life spans than large mammals (Van Valen, 1964: Coe, 1979; Western 1980; Damuth, 1982). However, this bias towards overrepresentation of small taxa is balanced, or outweighed, by complete environmental destruction of small skeletal elements caused in part by their greater surface area/volume ratios than larger skeletons (Behrensmeyer, 1978; Behrensmeyer et al., 1979; Korth, 1979). The reduction in numbers of small mammals available for fossilization evidently occurs quite rapidly in some environments, as Behrensmeyer et al. (1979) and Dechant and Behrensmeyer (1980) showed, and loss is most pronounced in mammals with living body weights of under 12 kg. Small mammals may be overrepresented relative to other members of the community if the assemblage is predator-related (Mellet, 1974; Korth, 1979; Behrensmeyer et. al, 1979; Vrba, 1980), and the fossil concentration is the result of accumulated carnivore scat.

Biases may also be caused by fluvial processes that not only selectively remove certain size ranges of a living population, but also contain allochthonous taxa. Catastrophic events are responsible for overrepresentation of some taxa and underrepresentation of others (Vrba, 1980).

In a given fossil deposit, any one, or all of, these factors may be responsible for biasing the initial death assemblage. Error in relative abundance counts is also often introduced by poor sampling techniques. The assumption is often made that small mammal remains can be adequately collected in surface collections, but in most cases this assumption is incorrect. Ideally, the best way to obtain all fossils present in a locality is to collect it in its entirety and

screenwash all the matrix for microfauna. Unfortunately, unless a site is a small isolated pocket, this procedure is about as feasible as counting all the animals in a living community. An alternative approach is similar to that used by modern ecologists to sample plants or animals in a community; collect random samples of bones and matrix from a portion of the site and make the assumption that the abundances of the animals found in them are representative of those found in the entire locality. This procedure was followed in the excavation of the Thomas Farm locality (Chapter 2). The total megafaunal and microfaunal abundances used in this chapter were obtained by combining MNI of taxa from the matrix samples of the three layers that were most similar taphonomically: units 5, 6, and 7. Megafaunal abundances were obtained by combining MNI of all megafaunal taxa (body mass > 1 kg) collected from layers 5 through 11 (Table 11-1).

The relationship of mammalian body size to population density of Recent mammals has been demonstrated by a number of workers, and can be described by the power function

$$A \quad W^a$$

where A is the abundance or population density, W is body mass, and a is the slope of the regression line of density on body mass. Damuth (1981) found that the value of a for Recent herbivores was -.75, Peters and Raelson (1984) showed that for temperate herbivores it was -.66, and Robinson and Redford (1986) arrived at a value of -.61 for Neotropical herbivore taxa. Recent carnivores, which have higher energy requirements than similarly sized herbivores (Peters and Raelson, 1984) have relatively lower population densities. Carnivore population density decreases at a more rapid rate with

increasing body size than does that of herbivores (Robinson and Redford, 1986) because home range size increases more rapidly with increasing body size. Body size/population density regression lines for carnivores have slopes that range from -.47 for large tropical carnivores (Peters and Raelson, 1984), to -.99 for Neotropical carnivores (Robinson and Redford, 1986) and -1.14 for temperate carnivores (Peters and Raelson, 1984).

Figures 11-1a and b and Table 11-1 show the abundances of fossil mammalian herbivores from Thomas Farm plotted against estimated body size. It is clear that the abundances of the fossils do not reflect the true population densities of the living animals. Damuth (1982) introduced a correction factor designed to eliminate the bias caused by pre-depositional surface destruction (Chapter 2, p .29). Figures 11-2a and b and Table 11-1 show the results of using the correction factor to estimate herbivore abundances. The matrix sample regression has a high R^2 value (Figure 11-2a), the larger total megafaunal sample has a lower R^2, but both possess similar slopes (-0.85 and -0.91, respectively). The absolute value of the slope of the line is higher than that of the population density/body mass regressions for Recent herbivores, because, as Damuth pointed out, the corrected fossil abundances reflect both population density and turnover rate. Life expectancy is also a function of body mass,

$$A \quad W^{(a + b)}$$

where a is the slope of the population density line, and b is the slope of the turnover line. Published values for the slope of this line range from -.27 (Damuth, 1982), to -.33 (Western, 1979). Therefore the slope of the population density regression for the

Thomas Farm herbivores is

$$a - b = -.90 - (-.30) = -.60.$$

Several conclusions may be drawn from these findings. First, the fossils from the Thomas Farm deposit have evidently been subjected to surface exposure destruction. Second, at least within the levels examined, other factors such as fluvial sorting have had relatively little effect in decreasing the abundances of the herbivores. Third, the mammalian herbivore assemblage from the locality is representative of the herbivore component of the once-living community. Animals that may have been more peripheral to the habitat should have abundance values that fall below the regression (for example, Diceratherium), those that for some reason were were more common than would be expected (Parahippus and Archaeohippus), have values that fall above the line.

The MNI of each carnivore species from Thomas Farm was plotted against the animal's estimated body mass (Figure 11-3a). As no relationship was discernable, it was necessary to use the correction factor for surface destruction (Damuth, 1982). The slope of the resulting line (Figure 11-3b) was considerably shallower than expected based on studies of Recent carnivore densities (Peters and Raelson, 1984; Robinson and Redford, 1986). The shallow slope of the regression line for fossil carnivores may be explained by several factors. Small carnivores appear to be underrepresented, as it has been reported that a 1 kg carnivore is about 1/10 as abundant as similarly sized herbivore in temperate regions, and about 1/3 as abundant in tropical regions (Peters and Raelson, 1984). The ratios of fossil small herbivore-to-small carnivore abundances, based on the

corrected values, are far higher than 10:1. In addition, body mass estimates for some of the carnivore species may not be accurate, and the fossil assemblage probably includes carnivores that were not actually a part of the community. The food requirements of carnivores often necessitate the maintenance of large home ranges (Harestead and Bunnell, 1979; Eisenberg, 1980, 1981). For this reason, carnivores may be recovered in fossil deposits in regions that were not normally part of their preferred habitat (Van Valen, 1964). These results indicate that any interpretation of the carnivore assemblage from Thomas Farm that is based on abundances should be approached with caution.

Species Interactions

It was noted previously that detailed analyses of competition and predation are not possible in a paleoecological study. However, there are some basic observations that may be made concerning the relationships of predator species to prey species. Prey density to predator density varies with body size, and with latitude (Eisenberg, 1980; Peters and Raelson, 1984), and even within a given population the ratio of densities is not constant. Comparison of densities between these two trophic levels requires more information than can be provided from a fossil site, particularly one in which the abundances of one of the groups (in this case the carnivores) does not reflect population densities of the living fauna. The traditional approach of calculating the ratio of fossil herbivore to fossil carnivore abundances (Shipman, 1981;144) has been shown to provide an innacurate means of calculating relative abundance relationships (Damuth, 1982; Peters and Raelson, 1984).

Chapters 5 and 9 contain general references to prey preferences of the carnivores from Thomas Farm. Studies on diets of Recent carnivores show that the size of the predator is correlated with the preferred size of prey taken (Rosenzweig, 1966, 1968; Vrba, 1980, Peters and Raelson, 1984). Rosenzweig (1966) plotted mean prey size, by rank, against body mass of Recent predators. The data appear to show a linear relationship if small mustelids, which eat disproportionately large prey for their body size (Rosenzweig, 1966; Ewer, 1973), are omitted. The regression calculated using data from Rosenzweig (1966) is shown in Figure 11-4. Body masses have been changed to kilograms and the Thomas Farm prey species are listed in their appropriate size categories on the left side of the graph. Placement of the Thomas Farm carnivore weights on the regression line provides an indication of the preferred prey of each of these animals. The canids Tomarctus canavus and Euoplocyon spissidens and the mustelid Oligobunis floridanus were all of similar body size, and may have had similar prey preferences. The graph shows that any number of small predators may have been involved in the formation of the unit 15 coprocoenosis discussed in chapter 5, although based on the type of bone breakage, the medium-sized canid Tomarctus canavus is the most likely candidate.

Ecological Diversity and Habitat

One approach to the analysis of fossil assemblages employs the concept that within a given community type, the number and distribution of "niches" available do not change appreciably over time. The animals that fill these niches (ecological spectra of Van Couvering, 1980) do change over time or may vary from one geographical

region to another. The concept of "trophic replacement" (Olson, 1966) within a community type has formed the basis of community analysis of fossil assemblages. One method of this type of analysis is a modification of an approach taken by ecologists to assess variation in ecological diversity across geographical or latitudinal gradients. Many of the studies investigated the trend toward increasing species diversity as latitude decreases (MacArthur, 1965, 1972). Harrison (1962) examined the diversity of food habitats among mammals in a neotropical rain forest. Fleming (1973) compared mammalian diversity in terms of taxonomic diversity, body size, locomotor type, and food habits of species inhabiting North temperate forests and Central American rain forests. Andrews et al. (1979) and Van Couvering (1980) recognized the usefulness of this approach for the comparison of Recent habitats to fossil assemblages. They employed methods similar to those used by Fleming to examine fossil and Recent mammalian communities of Africa. The advantage of an analysis of this type is that it does not take into account relative abundances of individuals, and therefore this bias does not need to be considered. The only requirements are that the assemblage not be particularly biased by taphonomic factors, and that the size of the known fauna provides good representation of the living fauna. The disadvantage of this approach is that sufficient material of each species should be available to allow assignment to a feeding or locomotor category. Incorrect assignments can lead to a misinterpretation of the community type represented by a fossil assemblage. Van Couvering (1980) has also cautioned against a too strict uniformitarian approach in the comparision of Recent and fossil communities, as community types may

not be static over time, but undergo evolution as do species. The mammalian fauna from the Thomas Farm locality will be compared with mammalian assemblages inhabiting North and Central American forest communities, ranging from north temperate to tropical, based on Fleming's 1973 study. The fossil assemblage will also be compared to the fossil and Recent mammalian communities analyzed by Andrews et al. (1979) and Van Couvering (1980). Diversity of the mammals within four categories: taxonomic, body size, locomotion, and food habits, will be discussed.

Number of Species per Order

The histogram showing percentages of species per mammalian order at Thomas Farm is distinctive in the high proportions of carnivores, artiodactyls, and bats. The shape of the histogram bears little resemblance to histograms of species abundances per order from New World forests, which possess relatively few species of large ungulates (Harrison, 1962; Fleming, 1973; Emmons, 1984). Comparisons with New World forest communities show that the taxonomic distribution of species within a temperate deciduous forest in Tennessee is most similar to that seen in the fossil locality (Figure 11-5a), although the proportions of the Thomas Farm fauna are significantly different ($P = 0.01$) from those of the recent fauna (Chi-square = 122.3 at 4 d.f.).

It is difficult to directly compare a North American fossil site to a Recent African community in terms of numbers of species per order, as taxonomic differences exist that are related to biogeography rather than to habitat differences (Figure 11-5b). Primates are absent from Miocene deposits in Florida, and are rare at other

localities where they occur in North America (MacDonald, 1963), but this group forms a significant part of the fauna in Africa. Andrews et al. (1979) also omitted bats from their study, but this order is common in the Thomas Farm deposit. If bats are omitted from consideration, the taxonomic diversity of Thomas Farm mammals bears some similarity to the composite histogram of several African woodland/bushland communities, although the two histograms are significantly different from one another (Chi-square = 26.1 at 5 d.f) at the P = 0.01 level. The similarities of the histograms are due primarily to the high proportions of artiodactyls and carnivores in the Recent African communities.

Body Size

As there are some general relationships between body size and taxonomic category, the body size histogram of Thomas Farm taxa is unlike those of Recent North and Central American forests (Figure 11-5c). Neotropical faunas are dominated by small taxa, in particular bats and small arboreal species (Fleming, 1973; Eisenberg, 1980; Emmons, 1984). The low representation of artiodactyls and carnivores in New World forest communties in the body size category is reflected in the low proportions of larger size mammals. It is likely that small mammals such as bats, rodents, and insectivores are underrepresented in terms of numbers of species preserved at the locality. The histogram of body sizes of Thomas Farm mammals is most similar to that of a northern Michigan deciduous forest, pictured in 11-5c, but is significantly different from it (Chi-square = 48.09 at 5 d.f.) at the 0.01 level.

The ranges and proportions of body sizes of mammals from African woodland/bushland habitats are also similar to the Thomas Farm histogram (Figure 11-5d). However, the proportions are signifcantly different (Chi-square = 25.6 at 3 d.f.) at the 0.01 level. The equatorial rainforest habitats are dominated by small taxa (Van Couvering, 1980). The Thomas Farm differs from the latter habitats in the low proportion of small taxa, which as mentioned above, may be due to preservational bias. The body size histogram for the Thomas Farm mammals is most similar to that of the Fort Ternan fossil locality (Andrews et al., 1979, Van Couvering, 1980:276), and is not significantly different from it at the 0.01 level (Chi-square = 4.81 at 4 d.f.). The Fort Ternan locality has been interpreted as a woodland/bushland community (Andrews et al., 1979).

Locomotor Zonation

It is very difficult to assign a fossil mammal to a particular locomotor category if postcranial material of the species is lacking. For this reason, the histograms of locomotor zonation are not as reliable in an analysis as are those of the previously discussed categories. The Recent New World tropical forests are characterized by a lack of large terrestrial mammals (Fleming, 1973), and by a large number of aerial (bats) and arboreal groups (Figure 11-6a). These types of mammals are notoriously underrepresented in most fossil deposits, and it is likely that they are underrepresented at the Thomas Farm locality as well. The locomotor zonation histogram of the Thomas Farm fauna is most similar to that of a Fairbanks, Alaska, or a Smokey Mountains, Tennessee deciduous forest, but is significantly

different from both at the P= 0.01 level (Chi-square = 17.42 and 18.32, respectively, at 4 d.f.).

It was difficult to assign fossil mammal species to the locomotor groups listed by Andrews et al. (1979). Determining what mammals might be classified as "small terrestrial mammals that climb vegetation" as opposed to scansorial or potentially arboreal forms on the basis of fossil remains was particularly hard. The Recent African communities that bear the most resemblance to the Thomas Farm locality in terms of type of locomotion of the mammals are deciduous woodlands, which have large numbers of large, terrestrial forms. The middle Miocene Fort Ternan site (Andrews et al., 1979; Van Couvering, 1980) and early Miocene Rusinga Hiwegi (Van Couvering, 1980) are both characterized by high proportions of large terrestrial mammals. In this respect, the Rusinga, interpreted by Van Couvering as a rain forest, is different from Recent rain forests in Africa. The Fort Ternan histogram, unlike the Recent woodland histogram, is not significantly different from the Thomas Farm histogram at the 0.01 level (Chi square = 14.8 as opposed to 21.43 at 4 d.f.).

Food Type

The Thomas Farm locality is characterized by a large number of browsing herbivores and carnivores. Mammalian insectivores (other than bats) and frugivores are rare, either because these members of the fauna were absent, or that these diets were not recognized in my assessment of food type class. The predominance of frugivores in the Neotropics is due primarily to the presence of phyllostomid bats in these regions (Koopman and Cockrum, 1967). This entire group of bats is absent from temperate North America both in fossil deposits and

Recent times, except for several specialized, non-frugivorous forms. The dietary preference histogram of the Thomas Farm mammals, when compared to those illustrated in Fleming (1973, also Figure 11-6c) is most similar to that of mammals in a forest in Fairbanks, Alaska, and is not significantly different from it at the P = 0.01 level (Chi square = 10.9 at 5 d.f.).

The Recent deciduous woodlands of Africa and the Thomas Farm locality possess similar ratios of herbivorous browsers to herbivorous grazers although the number of insectivorous species in the Recent environments is higher than that of the fossil locality (Figure 11-6d). The early Miocene Rusinga fauna also has a higher proportion of larger ground-dwelling browsers than do Recent forest environments (Van Couvering, 1980). Grazers predominate in the recent woodland/brushland and grassland habitats of Africa. The histogram in 11-6d is significantly different from that of the Thomas Farm histogram at the P = 0.01 level (Chi-square =29.3 at 5 d.f.).

Comparisons of the habitat spectra of Recent communities with the Thomas Farm assemblage provides conflicting results, and the major point that emerges is that The Thomas Farm does not closely resemble any one of the Recent communities discussed. This problem is due in part to the difficulties encountered in assigning fossil forms to ecological categories, and more importantly, to the fact that Recent New World environments, with their relative paucity of large ungulates and large carnivores, are not suitable for community comparisons with North American fossil localities. A third problem is that biases in faunal preservation probably account for much of the difference between the diversity histograms of the fossil localities and recent

communities. The fact that an African late Miocene fossil locality and the Thomas Farm locality are most similar in terms of several of the diveristy catagories illustrates this problem, rather than indicating that the environments of these two localities were extremely similar.

Ecological Diversity Indices

It is generally held that species diversity and equitability within a certain regional community type (forest, savanna, and so on) is constant, regardless of the specific community being examined (Fleming, 1973; Andrews et al., 1979). Within a given category (body size, locomotor, et cetera) the diversity can be measured using the Shannon-Weaver diversity index (Fleming, 1973; Andrews et al., 1979, Chapter 2, p. 30). Equitability of the distribution of the classes within the category is defined as

$$E = H'/H_{max}$$

where H_{max} is the natural log of the number of classes within the given category. Calculations of H' and E for the categories of body size, locomotor zonation, and food type of Thomas Farm mammals are shown in Table 11-2. These values may be compared with those of Recent communities (Fleming, 1973, and Andrews et al., 1979), keeping in mind the problems associated with comparing fossil and recent communities.

Comparision with North and Central America forests indicates that in terms of mammalian diversity in locomotor adapatations and body size ranges, the Thomas Farm is most similar to a southern North American temperate forest (Figure 11-7a). The greater diversity in food preferences resembles that seen in more tropical forests. The African

communities that are most similar to the Thomas Farm locality (11-7b) in terms of body size and food habits are the woodland/bushland habitats (Andrews et al., 1979). The Thomas Farm fauna differs from these in the low diversity of locomotor types, which as mentioned previously, is probably a function of the difficulty in assigning fossil mammals to the various classes.

Based on the above analysis, it appears that the Thomas Farm community was a temperate to subtropical woodland/bushland. The region was evidently not dominated by open plains, nor was it a tropical rainforest. A more complete picture of the environment can best be provided by summarizing the various lines of evidence provided by studies of the vertebrate fauna.

Habitat and Environment of Thomas Farm: Faunal Evidence

Herptetofauna

The amphibians, in particular the anurans, were covered in detail in chapter 6. A few points made in that chapter will be re-emphasized, and a few new ones made. The anuran fauna, in terms of number of species, is most similar to that seen in southeastern woodlands today (Bennett et al., 1980; Campbell and Christman, 1982). The diversity of anuran species known from the Thomas Farm also indicates that the climate was not extremely arid (Scott, 1976; Heatwole, 1982). The proportion of anurans to salamanders is characteristic of a subtropical climate. Salamanders are more diverse in north-temperate regions than they are in the southeastern United States (Duellman and Trueb, 1986). The presence of hylids indicates that the environment was characterized by wooded conditions, as this family is usually restricted to areas with fairly tall vegetation

(Conant, 1975). The large number of anurans preserved in the site indicates that water must have been nearby, as all the forms represented by fossils undoubtedly passed through an aquatic larval stage (Duellman and Trueb, 1986).

The reptile fauna requires more study. At present, relatively little can be inferred concerning habitat and environment based on what is known of the lizard and snake fauna (Auffenberg, 1963; Estes, 1963). The numbers of lizard species so far known are comparable to those of present day local Florida herpetofaunas (Campbell and Christman, 1982) and the diversity of taxa, as well as sheer numbers of individuals of lizards provide evidence that the climate was certainly no cooler than that of present-day northern Florida. Alligators, which were common in the Miocene of Florida, are also restricted to areas where the number of days with temperatures that fall below freezing are limited (Hibbard, 1960). The best evidence for a more equitable climate in the Florida early Miocene is provided by the presence of the land tortoise Geochelone tedwhitei. In a discussion of Pliocene and Pleistocene climates of the Great Plains, Hibbard (1960), showed that the Recent members of the genus Geochelone are restricted to climates where temperatures do not fall below freezing. It is unlikely that a Miocene Geochelone was able to do what its Recent relatives cannot: burrow or hibernate during cold spells. Thus the picture provided by the herpetofauna of the Thomas Farm locality is of a wooded region, with standing water present locally, perhaps on a seasonal basis. The climate may have been dry for part of the year, but overall was not much wetter or drier than present. The temperature was more tropical than today.

Mammalia

Chiroptera. The large and exciting bat fauna of Thomas Farm is currently under study, and the information presented here has been provided by G. Morgan. All of the bats known to date from the locality (Lawrence, 1943; G. Morgan, pers. comm.) are related to present-day insectivorous species that are obligate cave dwellers. The presence of these bats in large numbers in one specific layer (unit 15; see Chapter 3) of the site provides almost irrefutable evidence that at some stage in its development, the Thomas Farm locality was a cave or a series of caves. Evidence for a more tropical climate than today is provided by the presence of two families of bats, the Natalidae and Emballonuridae, that are entirely tropical in their present-day distribution. The Natalidae, or the funnel-eared bats, have a Neotropical distribution in lowland regions with moisture regimes that range from rainy to arid (Koopman and Cockrum, 1967). The Emballonuridae, or the sac-wing bats, are known from tropical environments of the New and Old World today. Members of this family may be found in a variety of habitats ranging from rainforest to desert (Koopman and Cockrum, 1967).

The absence of frugivorous bats from the Thomas Farm locality may be interpreted as evidence against a tropical climate in the Florida Miocene. Frugivorous bats are common in forest habitats of Central and South America. Their survival in an environment relies on the presence of a year-round supply of fruit (Fleming, 1973), a requirement that cannot be met in a seasonally cool climate. However, G. Morgan contends that the absence of frugivorous bats in the Florida Miocene may represent a biogeographic problem rather than an

environmental one. The family Phyllostomidae, to which all frugivorous neotropical bats belong, probably evolved in isolation in South America and may not have reached tropical North America until after the connection of North and South America in the late Pliocene.

Rodents. The presence of heteromyid rodents at Thomas Farm does not indicate that this region was an arid savanna or desert, as was believed in the past (Romer, 1948; Estes, 1963). The two species of heteromyid known from the locality are both most closely related to Central and South American forms that inhabit tropical to subtropical wooded regions ranging from rainforests to semi-arid woodland and bushland (Wood, 1932; Fleming, 1971). The absence of lagomorphs and rodents with high-crowned teeth indicates that grasses and coarse vegetation were not dominant forms of vegetation.

Carnivores and Ungulates. The absence of highly cursorial carnivores from Thoms Farm indicates that the environment must have been characterized by some type of wooded ground cover. The large numbers of browsing herbivores has been stressed previously, as their presence provides some of the best evidence for a woodland environment.

Floral Evidence

Sediments from Thomas Farm were examined for presence of pollen, but no evidence of pollen preservation was found. Plant fossil remains have been reported from one Florida Miocene locality, the Alum Bluff Formation in the Florida panhandle, some 300 km to the north of Thomas Farm (Berry, 1916). The age of the Formation was first considered to be late Oligocene or early Miocene (Berry, 1916, Barghoorn, 1951). Olsen (1964b) regarded the Alum Bluff as middle

Miocene, based on the presence of fragmentary equid remains that he assigned to Parahippus leonensis. Richard Hulbert (pers. comm.) examined these specimens, and places the age of the Alum Bluff from the middle Hemingfordian to the earliest Barstovian. This latest evidence indicates that the Alum Bluff is similar in age to the Thomas Farm locality, or perhaps slightly younger.

The paleoflora from Alum Bluff (Berry, 1916; Graham, 1964) consists of 4 plant types that today are strictly tropical in distribution, including breadfruit and satinwood. Several other species, such as Pisonia and camphor trees, are considered primarily tropical, but can survive in Florida today. The assemblage is dominated by several varieties of palms and palmettos, similar to those that are native to the southeastern United States today. The only species in the Alum Bluff flora that could be termed a temperate plant is the elm. Berry (1916) described the paleofauna as a tropical assemblage slowly being replaced by a subtropical to temperate flora. The assemblage represents two floral habitats, a lowland hammock, and a palmetto swamp. This sole paleoflora from the Miocene of Florida indicates that in the middle Miocene, conditions were more tropical than today, and that the panhandle (and perhaps further south and east) was dominated by woodlands and swamp habitats.

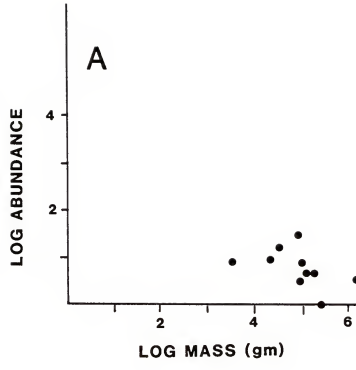
Conclusions

The previous pages documenting the taphonomic events and paleoecological reconstruction of the Thomas Farm locality may be outlined in a brief summary. Deposition at the locality, which was a high-walled sinkhole surrounded by woodlands, underwent several phases of deposition, including at least two wall collapses. In the early

stages of deposition, large and small animals were buried, and under the influence of a slight current in the (seasonally?) water-filled sink, some fluvial sorting and bone alignment occurred. The entire depositional process was attritional and not catastrophic. The final wall collapse exposed a cave system that was frequented by bats and mammalian and/or avian predators. Small mammal remains were preserved in carnivore scat, forming a coprocoenosis.

The area surrounding the sink was primarily wooded, although there may also have been some bushland or open habitats in the region as well. The range of yearly temperatures was probably less extreme and warmer than that of the area today; overall it must have been more tropical in character. Conditions may have been more arid than those in present-day Florida, or the climate may have been characterized by seasonal aridity, but there is not enough evidence to make any firm conclusions concerning this aspect of the environment.

Figure 11-1. Uncorrected raw abundances in MNI per species of herbivore taxa from Thomas Farm plotted against body mass. a) Megafauna from units 5-11; b) All taxa from combined random samples of units 5, 6, and 7.


A
LOG ABUNDANCE
4
2
2
4
6
LOG MASS (gm)

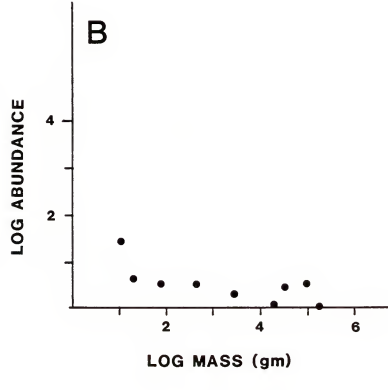
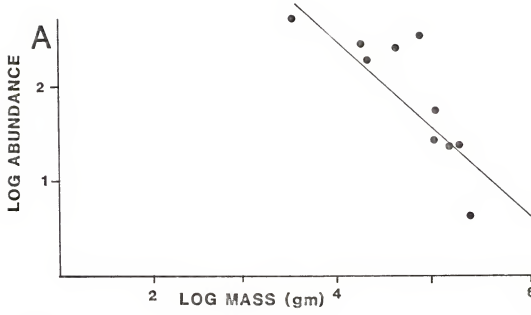

B
LOG ABUNDANCE
4
2
2
4
6
LOG MASS (gm)

Figure 11-2. Corrected raw abundances in MNI per species of herbivore taxa from Thomas Farm plotted against body mass. a) Megafauna from units 5-11; b) All taxa from combined random samples of units 5, 6, and 7.


A
LOG ABUNDANCE
2
1
2
LOG MASS (gm)
4
6

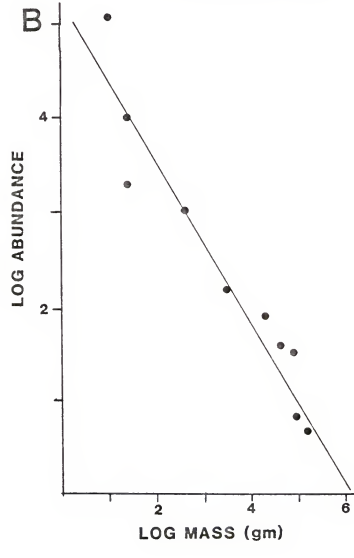
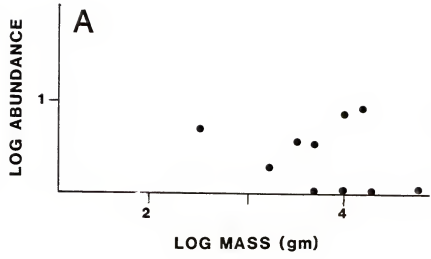

B
LOG ABUNDANCE
4
2
2
4
6
LOG MASS (gm)

Figure 11-3. Relative abundances, in MNI per species, of carnivore taxa from combined random samples of units 5, 6, 7. a) Uncorrected raw abundances; b) Corrected raw abundances.


A
LOG ABUNDANCE
1
2
4
LOG MASS (gm)

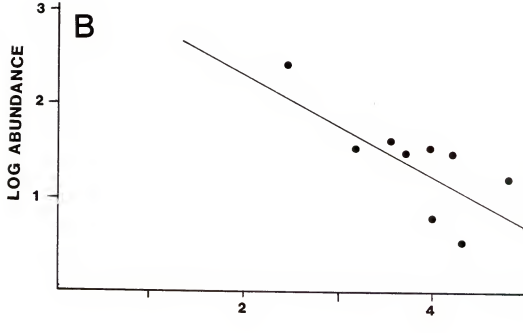

B
LOG ABUNDANCE
3
2
1
2
4

Figure 11-4. Regression of mammalian carnivore body mass on mean prey size. Raw data from Rosenzweig, 1966. Abbreviations: A, Amphicyon; Cy, Cynodesmus; Cyl, Cynelos; E, Euoplocyon; H, Hemicyon; L, Leptarctus; M, Mustelidae; O, Oligobunis; To, Tomarctus. Line calculated by least squares regression;
Food rank = (1.63) (log predator body mass) + 0.529.
Closed circles indicate values for recent carnivores.

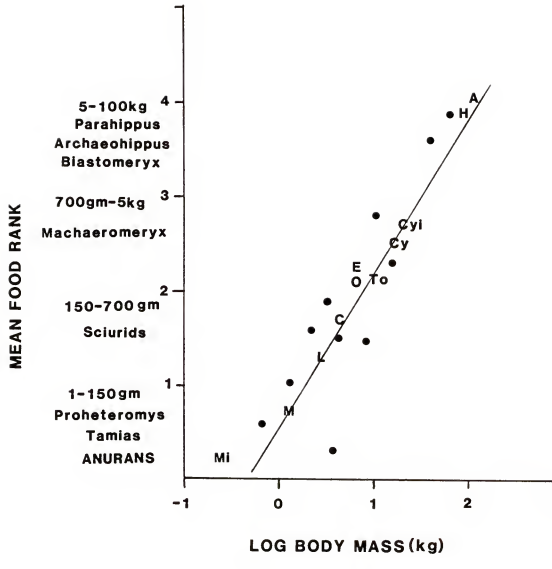

MEAN FOOD RANK
5-100kg
Parahippus
Archaeohippus
Blastomeryx
700gm-5kg
Machaeromeryx
150-700gm
Sciurids
1-150gm
Proheteromys
Tamias
ANURANS
4
3
2
1
A
H
Cyi
Cy
E
O
To
C
L
M
Mi
-1
0
1
2
3
LOG BODY MASS (kg)

Figure 11-5. a) Taxonomic group histogram of Thomas Farm mammals compared to taxonomic group histogram of mammals from northern temperate deciduous forests (after Fleming, 1973); b) Taxonomic group histogram of Thomas Farm mammals compared to taxonomic group histogram of mammals from African woodland/bushland habitats (after Andrews et al., 1979). Thomas Farm[1] is histogram with bats omitted; c) Body size histogram of Thomas Farm mammals compared to body size histogram of mammals from northern temperate deciduous forests (after Fleming, 1973); d) Body size histogram of Thomas Farm mammals compared to body size histogram of mammals from African woodland/bushland habitats and from the Fort Ternan fossil locality (after Andrews et al., 1979). Abbreviations: A, artiodactyls; B, bats; C, carnivores; I, insectivores, O, other; P, primates; R, rodents; a = <100g; b = 100g-1000g; c = 1000g-10,000g; d = >10,000g; 1 = <1kg; 2 = 1kg-10kg; 3 = 11kg-45kg; 4 = 45kg-180kg; 5 = >180kg.

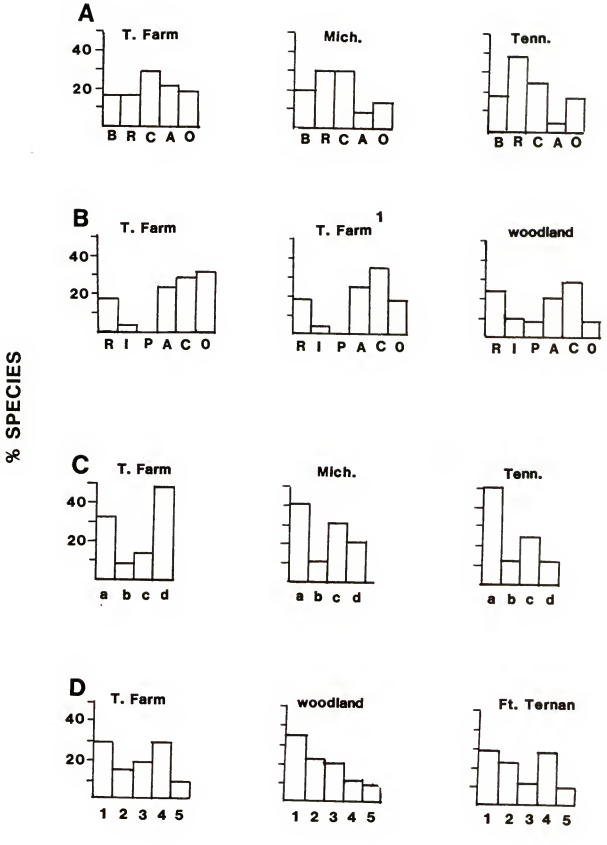

A
T. Farm
Mich.
Tenn.
40
20
B R C A O
B
T. Farm
T. Farm 1
woodland
R I P A C O
C
T. Farm
Mich.
Tenn.
a b c d
D
T. Farm
woodland
Ft. Ternan
1 2 3 4 5
% SPECIES

Figure 11-6. a) Locomotor group histogram of Thomas Farm mammals compared to locomotor group histogram of mammals from northern temperate deciduous forests (after Fleming, 1973); b) Locomotor group histogram of Thomas Farm mammals compared to locomotor group histogram of mammals from African woodland/bushland habitats and from the Fort Ternan locality (after Andrews et al., 1979); c) Food habit histogram of Thomas Farm mammals compared to food habit histogram of mammals from northern temperate deciduous forests (after Fleming, 1973); d) Food habit histogram of Thomas Farm mammals compared to food habit histogram of mammals from African woodland/bushland habitats.
Abbreviations: A, arboreal; F, fossorial; S, scansorial; T, terrestrial; T_1, terrestrial large mammal; T_2, terrestrial small mammal; V, volant or aerial; W= water-dwelling or aquatic; c, carnivore; f, frugivore, g, granivore, h, herbivore; h_b, browsing herbivore; h_g, grasing herbivore; i, insectivore; o, omnivore.

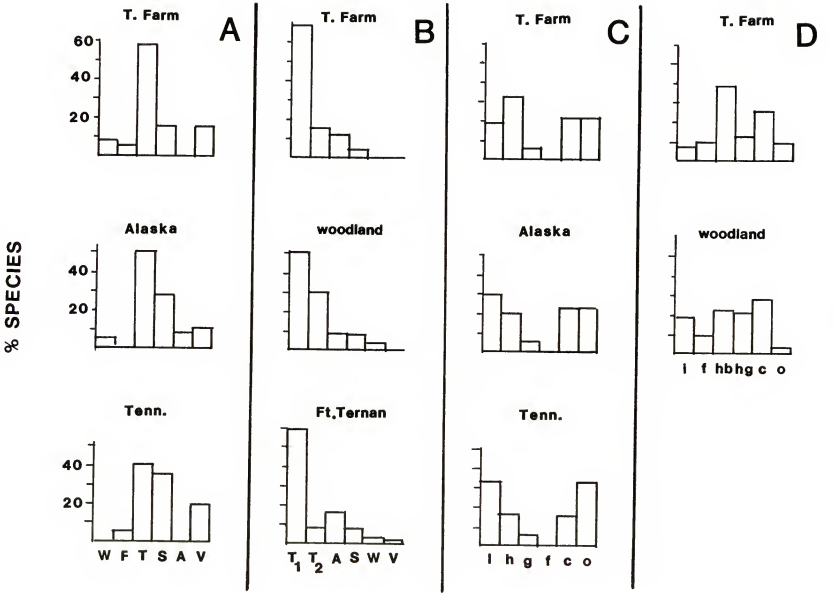
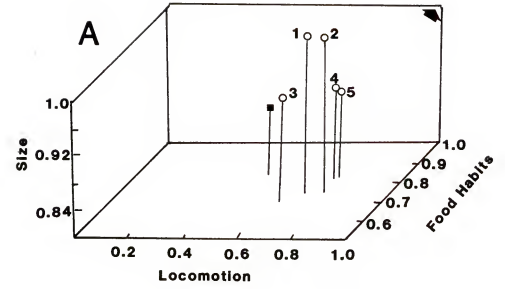

% SPECIES
A
B
C
D
T. Farm
Alaska
Tenn.
woodland
Ft.Ternan
60
40
20
W F T S A V
T1 T2 A S W V
l h g f c o
l f hbhg c o

Figure 11-7. Ecological diversity of modern and fossil mammal communities showing diversity indices for locomotor adaptation, food habits, and body size. Arrows indicate point of maximum diversity. a) Northern and Central American forests (from Fleming, 1973). 1, Fairbanks, Alaska white spruce-paper birch forest; 2, Warren Woods, Michigan deciduous beech-maple forest; 3, Great Smokey Mountains, Tennessee deciuous beech-maple forest; 4, Balboa, Panama dry tropical forest; Cristobal, Panama moist tropical forest; black square, Thomas Farm; b) African fossil and recent habitats. Closed circles, recent woodland/bushlands; open square, Fort Ternan locality; closed square, Thomas Farm locality.


A
1
2
3
4
5
1.0
0.92
0.84
Size
0.2
0.4
0.6
0.8
1.0
Locomotion
1.0
0.9
0.8
0.7
0.6
Food Habits

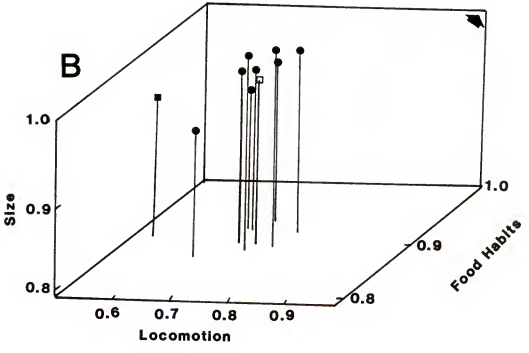

B
1.0
0.9
0.8
Size
0.6
0.7
0.8
0.9
Locomotion
1.0
0.9
0.8
Food Habits

Table 11-1. Abundances of vertebrates from Thomas Farm.

A.) Body mass estimates, raw abundances and corrected abundances for megafaunal taxa from units 5,6 7,8, and 11. Abbreviations; W = body mass in grams, A_{raw}= actual abundances, d_1= correction value for surface destruction, A corr = A_{raw} times d_1.

Species	W	A (raw)	d_1	A (corr)
Machaeromeryx gilchristensis	3,000	7	69.6	483
Blastomeryx floridanus	20,000	9	18.9	171
Archaeohippus blackbergi	39,000	20	12.1	241
Parahippus leonensis	75,000	33	7.7	257
Floridatragulus dolicanthereus	100,000	4	6.3	25
Prosynthetoceras texanus	100,000	8	6.3	51
Anchitherium clarenci	130,000	4	5.3	21
Nothokemas floridanus	160,000	5	4.6	22
Diceratherium barbouri	220,000	1	3.7	4
Floridaceros whitei	1,500,000	4	1	4
Miomustela sp.	300	5	51.1	256
Small mustelid	1,500	2	17.1	34
Leptarctus ancipidens	3,552	4	9.5	38
Small canid	5,000	4	7.6	30
Oligobunis floridanus	9,755	1	4.8	5
Euoplocyon spissidens	9,000	0		
Tomarctus canavus	9,500	7	4.8	34
Cynodesmus jamonensis	15,000	8	3.6	29
Cynelos caroniavorous	19,500	1	2.9	3
Hemicyon johnhenryi	75,000	1	1.2	1
Amphicyon longiramus	98,000	6	1	6

B.) Body mass estimates, raw abundances, and corrected abundances for herbivore taxa from combined random sample of units 5, 6, 7. See text for further explanation.

	W	A(raw)	d_1	A(corr)
Proheteromys floridanus	10	34	3329.6	113208
small sciurid	48	5	1894.9	9474
Eomyid	48	1	1894.9	1895
Proheteromys magnus	87	6	752.3	4513
Large sciurid	237	4	251.4	1005
Machaeromeryx gilchristensis		2		139
Blastomeryx floridanus		1		76
Archaeohippus blackbergi		3		36
Parahippus leonensis		4		31
Floridatragulus dolicanthereus		1		6
Prosynthetoceras texanus		1		6
Anchitherium clarenci		1		5
Nothokemas floridanus		1		5
Diceratherium barbouri		0		0
Floridaceros whitei		1		1

Table 11-2. Ecological diversity indices based on number of species per class of each diversity category. See text for more complete explanation. Columns headed Fleming are indices based on categories used by Fleming, 1973; those headed Andrews are indices based on categories used in Andrews et al, 1979.

Category	H'(Fleming)	E(Fleming)	H'(Andrews)	E(Andrews)
Body Size	1.46	.90	1.54	.96
Locomotion	.93	.52	.90	.50
Food Habit	1.49	.83	1.59	.89

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BIOGRAPHICAL SKETCH

Ann E. Pratt was born January 28, 1953 in Worcester, Massachusetts. She grew up in Worcester, graduating from Burncoat Senior High School in June of 1971. She attended Clark University, also in Worcester, where she majored in zoology. She received a B.S. degree from that institution in December of 1974. She spent the following 2 years working on Cape Cod, Massachusetts. In January of 1977, she enrolled in the master's degree program in the Department of Zoology, University of Massachusetts, and received her M.S. in August of 1979. Since August of 1979, she has attended the University of Florida, graduating from that institution with a Ph.D. in December of 1986.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ronald G. Wolff, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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December 1986

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